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BULLETIN
OF THE
TORREY BOTANICAL CLUB

VOLUME 67 MARCH · 1940 NUMBER 3

Inflorescence, Floral anatomy and Morphology of Leitneria floridana *

ERNST C. ABBE AND T. T. EARLE

(WITH 37 FIGURES)

INTRODUCTION

This study of the perennially puzzling family, the *Leitneriaceae*, was undertaken with two related objectives in mind. The more important of these was felt to be an evaluation on an anatomical basis of the morphology of the much reduced flower and inflorescence. The desirability of a re-examination of the family from this point of view was suggested by the better understanding of the floral and inflorescence morphology of other amentiferous families which has followed a careful examination of their vascular anatomy (Fisher, 1928; Abbe, 1935, 1938). The second objective was to circumscribe somewhat, the colorful wanderings of the family in the various phylogenetic "systems." Until much more is known about the Angiosperms this latter objective must remain largely the expression of a pious hope, nevertheless it seems to the writers that certain broad lines of relationship suggest themselves upon a re-evaluation of the available evidence.

A few words of general information concerning the family may well be introduced at this point. The family consists of the single species, *Leitneria floridana* Chapm., which occurs in isolated fresh- or brackish-water swamps and sloughs in parts of Florida, Georgia, Arkansas, Missouri, and Texas (Sargent, 1926). The plant is a shrub or small tree up to twenty feet in height, with pale, fissured bark and with thick and firm leaves, which are bright green above and below are pale and coated with

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a villous pubescence. The wood is soft and exceedingly light, the character to which the plant owes its common name of "Cork Wood."

MATERIALS AND METHODS

The writers are indebted to the late Professor Duncan S. Johnson, of Johns Hopkins University, who kindly collected the staminate and pistillate inflorescences used in this investigation. The trees which were the source of the material grow on the Johns Hopkins University campus. The fixing fluid was a chrom-acetic mixture. The material was subsequently stored in 70 per cent alcohol. Prior to detailed investigation the inflorescences were transferred to distilled water and permitted to soak for some time, which facilitated dissection. Representative dissections were drawn to scale and then were run up through the usual N-butyl alcohol series. Serial sections, 9 micra in thickness, were made and were stained with crystal violet and erythrosin in all series except one, which was stained with safranin and fast green. Camera lucida drawings of the sections were made and from these the three-dimensional figures were reconstructed to scale.

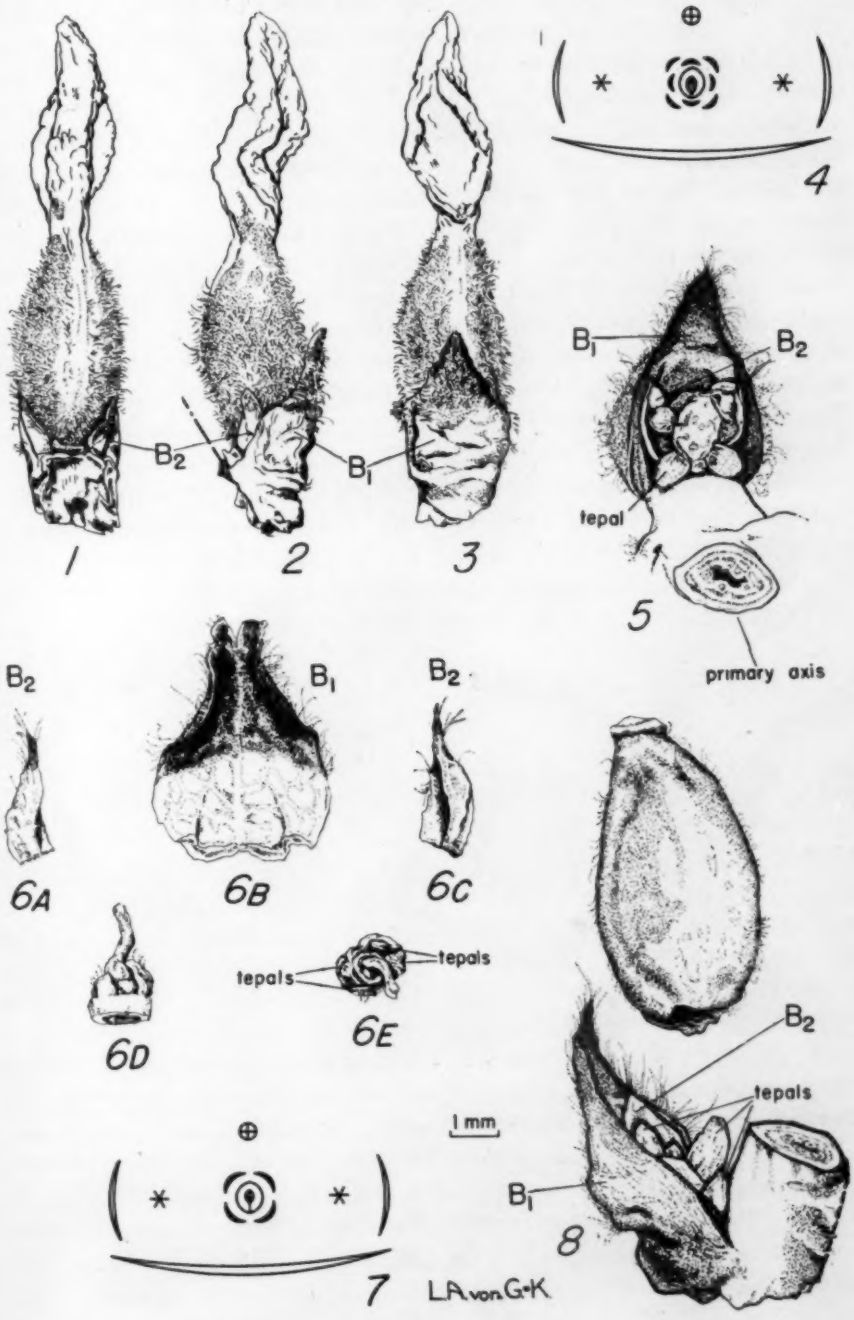
PISTILLATE FLORETS AND INFLORESCENCES

External Morphology.—At the time of pollination the pistillate flowers are sessile and solitary in the axils of the relatively large, spirally arranged primary bracts, each floret being flanked by two smaller secondary bracts. The primary axis of the inflorescence is stiffly erect. Owing to the combination of large overlapping bracts and small flowers the term ament would be completely applicable to the pistillate inflorescence if it were not for this stiff primary axis. The whole inflorescence may therefore be considered a "spike-like" ament. After pollination there is a recognizable lengthening of the secondary axes too slight to justify a change in the designation of the inflorescence. While most of the primary bracts of the inflorescence have pistillate flowers in their axils, the last two or three at the apex, and a still larger number at the base have no flowers in their axils.

Explanation of Figures 1–8

Figs. 1–8. Habit sketches and floral diagrams of pistillate flowers and cymules of *Leitneria floridana*. Figs. 1–3. Adaxial (dorsal), lateral, and abaxial (ventral) views, respectively, of a pistillate cymule from the upper part of a spike. Fig. 4. Floral diagram of following figure. Fig. 5. Dorsal view of axil of primary bract (B_1); pistil removed; secondary bracts (B_2), tepals, and region of attachment of pistil visible. Fig. 6A–6E. Dissected pistillate cymule. 6A. Secondary bract; 6B. Primary bract; 6C. Secondary bract; 6D and 6E. Young pistil with tepals, showing the short pedicel of the flower. Fig. 7. Floral diagram of the following figure. Fig. 8. Pistillate cymule (the pistil "lifted out").

All figures to the same scale. Note scale between Figs. 7 and 8.


B2
B1
1
2
3
4
B1
B2
tepal
5
primary axis
B2
B1
B2
6A
6B
6C
6D
tepals
tepals
6E
1 mm
B2
tepals
B1
8
7
L.A. von G.-K.

The individual pistillate floret (figs. 1–3, 6D–E, 8) consists of a simple pistil surrounded at the base by very small tepals (figs. 5, 8). The placenta is on the abaxial side of the pistil, and bears a single anatropous ovule, which is attached toward the upper end of the placenta. The ovary is narrowly ovate in form, and is covered with dense short, crisp pubescence, which is practically absent in a narrow median longitudinal line on both the adaxial (fig. 1) and the abaxial (fig. 3) sides of the ovary. The ovary is crowned with a prominent fleshy stigma (figs. 1–3), which is lost by abscission at the base soon after fertilization (fig. 8).

Surrounding the base of the ovary is a perigon composed of diminutive tepals varying in number from three to about eight (figs. 4–5). The usual complement is four (figs. 6E, 7), in the diagonal radii. The tepals are inserted at the end of an extremely short pedicel, or secondary axis. Attached to this secondary axis there are consistently, in our material, two opposite secondary bracts (B_2, figs. 1, 2, 5, 6A, 6C, 8).

The writers found no evidence of vestigial stamens in the forty or fifty pistillate flowers which they examined. Further observations, however, might substantiate Baillon's (1880) report of bisexual florets.

Vascular Anatomy.—The primary axis of the pistillate inflorescence has a vascular cylinder broken up by the elongate combined leaf and branch gaps which results in a marked dictyostelic condition (fig. 22). From the base of each gap there arises the primary bract bundle (B_1) which passes through the cortex of the primary axis (fig. 22 level A), and of the secondary axis. Soon after the primary bract becomes free from the axis of the ament (fig. 22, level C) the primary bract bundle breaks up abruptly into a number of minor branches, which anastomose with each other (fig. 6B). Occasionally a minor anastomosis may connect the primary bract bundle with the vascular system of the secondary axis, or there may be some branching and recombining on the way out to the primary bract (fig. 22, between levels A and B), but this does not obscure its course. Whether the anastomoses are an indication of the suppression of the lateral bundles is not clear.

From either side of the combined leaf and branch gap in the primary axis there departs a branch trace. The two branch traces, one or the other of which may split (fig. 22, level A) and recombine almost immediately in the cortex of the primary axis, broaden somewhat to form two arcs (in transverse section, between levels A and B) as they pass into the secondary axis. These arcs are separated by abaxial and adaxial gaps which fail to close until after the lateral departure of the secondary bract bundles (B_2). The vascular system of the secondary axis thus becomes four-parted immediately after the departure of the secondary bract bundles.

These four bundles of the secondary axis form a dictyostele which becomes the vascular cylinder of the pedicel of the solitary floret (level B). The bundles, after a short distance, as a result of the closing of the gaps, form a loose cylinder of vascular tissue. This promptly breaks up again to form five bundles (fig. 22, between levels B and C), the abaxial ones very quickly uniting to form the compound ventral bundle (*vn*, level C) of the simple pistil. The adaxial bundle becomes the dorsal bundle (*dr*, level C) of the pistil, and continues unbroken (except for minor anastomoses) throughout the length of the pistil to form one of the three bundles of the stigma (level E). The two remaining bundles (level C) at the base of the ovary are so frequently associated with the dorsal in their origin that their interpretation as branches of the dorsal seems justifiable, although they sometimes become distinct at the same level as do the dorsal and ventrals.

A relatively infrequent occurrence, noted in only two cases, was the development abaxially in the median plane of a definite, but short-lived diminutive bundle (fig. 22, *ves* 3, between levels B and C) from a gap, whose sides ultimately continue on to form the ventrals of the pistil. This bundle (*ves* 3) the writers are inclined to interpret as a vestige of the vascular supply to a second carpel, although this must remain as an inference only, since there is no external evidence of a second carpel in the material studied. Vestigial 3 could also be interpreted as a continuation of the vascular tissue of the floral axis.

Almost immediately after the union of the two ventrals to form the fusion ventral (*vn*, fig. 22, just above level B), one or both of the branches of the dorsal splits (fig. 22, just above level C), one-half anastomosing with the fusion ventral, and the other half forming a lateral branch *y*. From the place of union of half of the branch of the dorsal with the fusion ventral there arises a small bundle *x*. The bundles *x* and *y* then branch repeatedly throughout the wall of the ovary, anastomosing with each other, and with the fusion ventral and dorsal to form the network of bundles characteristic of the fruit of *Leitneria*. The greater part of this anastomosing network is omitted from the reconstruction since it obscures the more important features.

This pattern of branching of the vascular tissue is quite remarkable, and has been well illustrated (Heim, 1892; Sargent, 1895 and 1926; Trelease, 1895). It resembles the similar, but less extensive, anastomosing vascular tissue which occurs in the ovary walls of mature fruits of the magnoliaceous genus, *Illicium*.

Except for the minor anastomoses which develop between the fusion ventral and the vascular network of the ovary wall, there are but few changes in the course of the fusion ventral to the stigma. Sometimes a

small branch develops (fig. 22, *ves* 2) which continues adaxially for a short distance in the median plane from near the base of the fusion ventral. This may well be a vestigial ovule bundle, although no evidence was noted of the occurrence of any such ovule in our material. As the fusion ventral continues toward the upper end of the ovary it broadens slightly. When it is approximately opposite the upper limit of the loculus it divides into three branches. The two lateral bundles, which evidently represent the original ventrals, continue on into the stigma, forming two of its three bundles. The bundle between the two ventrals bends abruptly downward and for a short distance travels in the wall of the ovary parallel to the fusion ventral. At the funiculus, the bundle gently bends adaxially and continues downward into the ovule. Soon after it enters the ovule it splits into three major branches, the outer branches of which continue unbroken to the chalaza of the ovule. The central bundle frays out into four or five smaller bundles which also terminate at the base of the ovule. No evidence was found of vascular bundles elsewhere in the ovule at this stage of development (shortly after fertilization). In one case, just above the funiculus, the ovule bundle developed a branch (fig. 22, *ves* 1) which ran for a short distance downward into the ovary wall between the fusion ventral and the ovule bundle. Its significance is not clear, although in our opinion it could well be interpreted as an aborted ovule bundle, since a second ovule might be expected to arise from the other margin of the carpel.

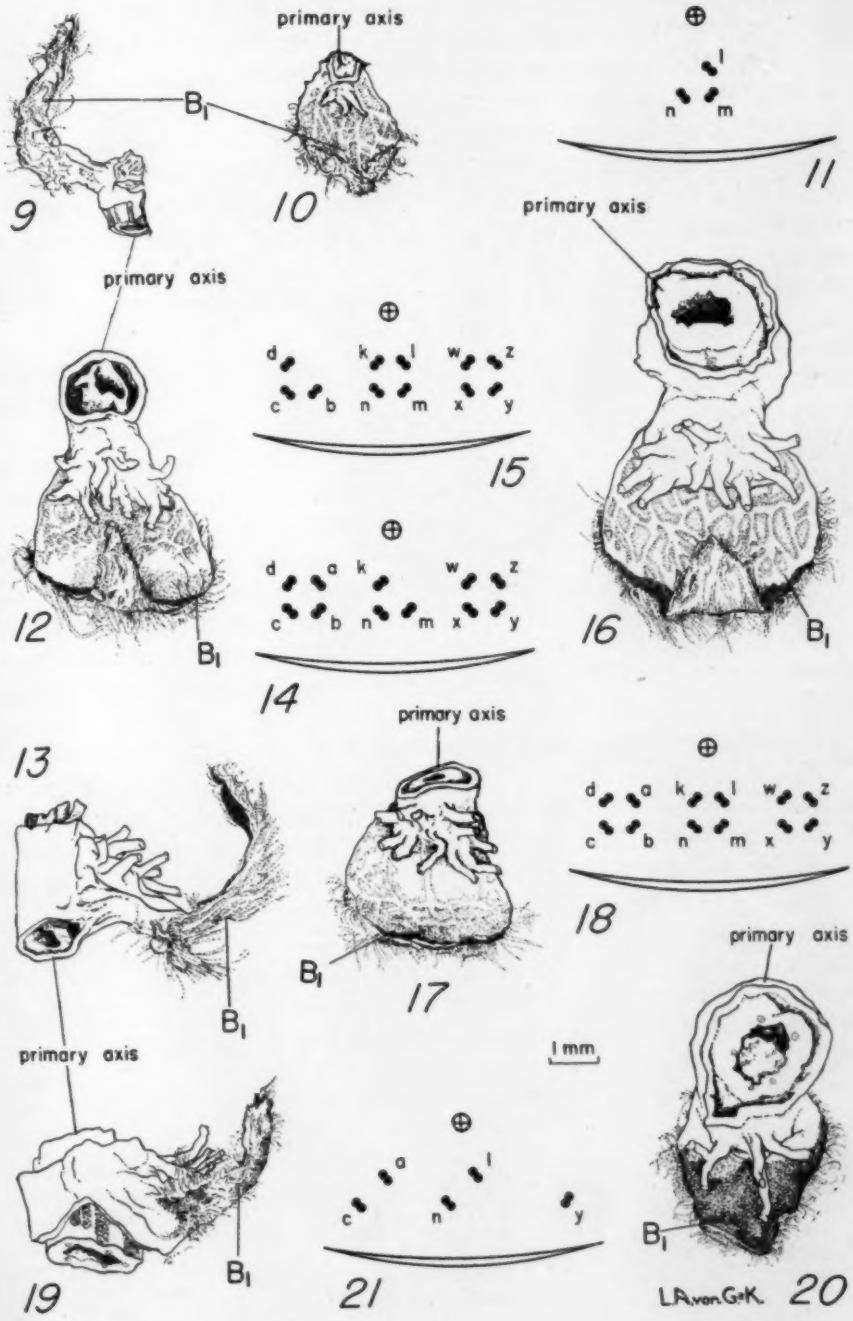
Mention should be made of the sporadic occurrence of isolated vascular bundles in the tepals. In several florets xylem composed of but one or two tracheids was observed towards the distal end of one or two of the tepals. In no case was there a connection of these traces with the vascular system of the pedicel. A similar case of an isolated bundle was noted in one of the smaller secondary bracts.

STAMINATE FLORETS AND INFLORESCENCES

External Morphology.—The staminate inflorescence consists of 40–50 cymules situated in the axils of large, spirally arranged, primary bracts.

Explanation of Figures 9–21

Figs. 9–21. Figs. 9, 10. Reduced staminate cymule from terminal portion of inflorescence. Fig. 11. Floral diagram of cymule shown in preceding figures. Figs. 12, 13. Dorsal and lateral views of staminate cymule from central portion of inflorescence. Fig. 14. Floral diagram of preceding figures. Fig. 15. Floral diagram of following figure. Fig. 16. Dorsal view of staminate cymule from central portion of inflorescence. Figs. 17, 19. Dorsal and lateral views, respectively, of staminate cymule from lower portion of inflorescence. Fig. 18. Floral diagram of cymule shown in figures 17 and 19. Fig. 20. Dorsal view of staminate cymule from lower portion of inflorescence. Fig. 21. Floral diagram of preceding figure. All figures to the same scale as in Figs. 1–8.


primary axis
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primary axis
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w
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primary axis
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B1
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18
primary axis
primary axis
1 mm
B1
19
B1
a
l
c
n
y
21
B1
L.A. von G. K.
20

Secondary bracts are absent. Unlike the pistillate inflorescence, the primary axis of the staminate inflorescence is lax, characteristic of a true ament. The bracts are covered on their abaxial surface with a dense growth of glandular pubescence. Van Tieghem and LeComte (1886) have reported as many as 15 stamens in the axils of the bracts but in our material the cymules contain from 3 to 12 stamens each. The number of stamens largely depends on the location of the cymule in the ament, being least toward the basal and apical regions. At the extreme base and apex the primary bracts are entirely devoid of stamens. Baillon (1880) has reported the presence of small, unequal bracts surrounding the stamens, sometimes united to form a small perianth, but no evidence of these structures has been found in our material, either externally or in the distributional pattern of its vascular tissue.

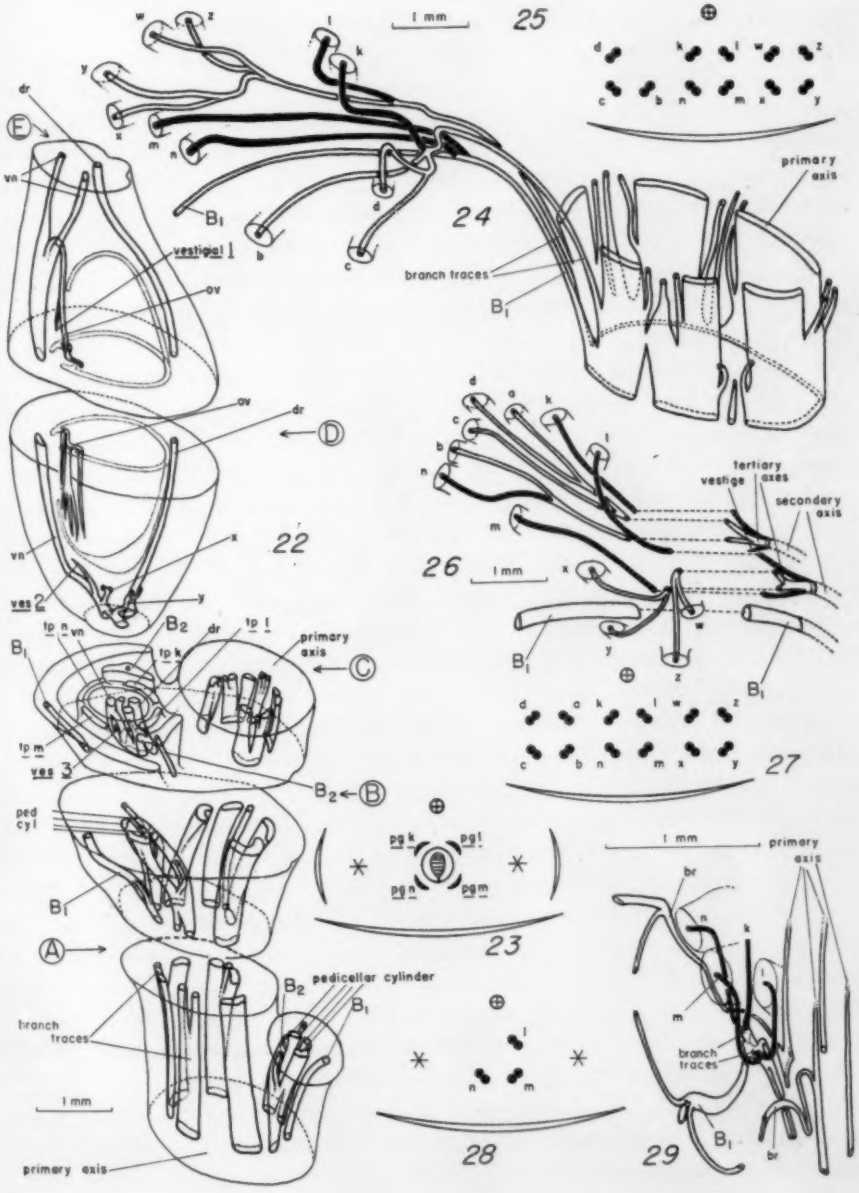
The cymules in the central part of the ament usually consist of 10–12 stamens, arranged in three groups (figs. 12, 16, 17). The justification of assigning the stamens to three groups on the basis of external morphology will be seen when the vascular anatomy of the staminate cymule is described. It is sometimes difficult to place a particular stamen in a particular floret, because of the crowding of the three florets in the cymule, but the position is usually made clear when the internal anatomy is examined, as will be shown subsequently. Even in the apical (figs. 9, 10) and basal (figs. 19, 20) cymules, which consist of a greatly reduced number of stamens, the allocation of the various stamens to particular florets is facilitated by an examination of the vascular anatomy of the cymule.

Vascular Anatomy.—The vascular cylinder of the primary axis is broken by the many leaf and branch gaps into a dictyostele (fig. 24). The cymules in the lower region of the ament show the least modification in their vascular anatomy. Figure 26 is a reconstruction of the vascular system of a cymule from the lower part of an ament. The trace to the primary bract (B_1) passes out from the primary axis and is unbranched in the bract until it is beyond the region where the branch bundles terminate

Explanation of Figures 22–29

Figs. 22–29. Reconstructions of the vascular systems of pistillate and staminate florets and cymules. Fig. 22. A composite three-dimensional reconstruction of a pistillate floret and cymule, from the central portion of the spike. Fig. 23. Floral diagram of the cymule shown in preceding figure. Fig. 24. Three-dimensional reconstruction of staminate cymule from central part of an ament (cf. Fig. 16). Fig. 25. Floral diagram of cymule shown in preceding figure. Fig. 26. Three-dimensional reconstruction of staminate cymule from lower part of an ament (cf. Fig. 17). Fig. 27. Floral diagram of preceding figure. Fig. 28. Floral diagram of following figure. Fig. 29. Three-dimensional reconstruction of greatly modified staminate cymule from terminal portion of ament (cf. Figs. 9 and 10).

The scale of each reconstruction is shown by a line equivalent in length to 1 mm. near each figure.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primary axis
branch traces
vestigial 1
ovary
dorsal
ventral
22
vestigial 2
tp n
tp k
tp l
tp m
vestigial 3
primary axis
ped cyl
pedicellar cylinder
branch traces
primary axis
26
tertiary vestige
secondary axis
27
pg k
pg l
pg n
pg m
23
28
29
br
branch traces

in the stamens, and it then breaks up into smaller bundles (cf. fig. 16).

Arising from each side of the gap are the two branch traces, which pass out in a gentle curve toward the group of stamens representing the cymule. These two arcs of vascular tissue represent the vascular system of the secondary axis. As soon as these arcs arrive in the base of the primary bract each forms a large central branch, flanked by two small branches. The small branches continue in an abaxial direction while the large central branches diverge abruptly to supply the lateral groups of stamens. Topographically, these large branches represent the vascular supplies to the tertiary axes, which, in the absence of secondary bracts, fill the gap at their origin. A short distance out from their origin they branch more or less dichotomously to supply the four stamens of each of the lateral florets.

The small bundles which arise on either side of the supply to the tertiary axes represent the continuation of the secondary axis and continue more or less in the median region, ultimately supplying the stamens of the secondary floret. In the cymule illustrated (fig. 26) the bundle labelled *vestige* continues for but a short distance and fails to supply a stamen. The stamen *n*, whose position suggests that it belongs to the secondary floret, receives its vascular supply as a branch from the trace to one of the stamens (*b*) of a tertiary floret. If stamen *n* is a member of the secondary floret, its vascular supply has anastomosed with that of the tertiary florets, an occurrence which is not without precedent in concentrated inflorescences of this type. That its origin should remain as a stub is somewhat unexpected, however. An alternative explanation would be to attribute a pentamerous state to one of the tertiary florets, and a trimerous one to the secondary floret, also not inconceivable, although not in keeping with our observations of the cymules in our material. We are inclined to adopt the former explanation, but with the reservation that the evidence is not conclusive.

The vascular system of a characteristic cymule from the central portion of an ament is shown in figure 24. This differs from the staminate cymule already described in the specific modifications which are associated with the vascular supply to the secondary floret. Two of the stamens, *m* and *n*, receive their supplies as branches from the primary bract bundle (B_1), a result of the transfer by fusion of the stamen bundles to the primary bract bundle. This is not an isolated instance as is shown by an analogous occurrence in the staminate cymules of *Corylus* (Abbe, 1935), in which the more modified cymules show this same relationship between the supply to the secondary floret and the primary bract trace. To return to *Leitneria*, the other two stamens, *k* and *l*, of the secondary floret have a less modified relationship to the remainder of the vascular system, in that they

merely depart rather tardily from the supply to the tertiary florets. With the less modified condition shown in figure 26 as an intermediate, there can hardly be any question that the average or more usual condition shown in figure 24 is but slightly modified and represents a triflorous cymule.

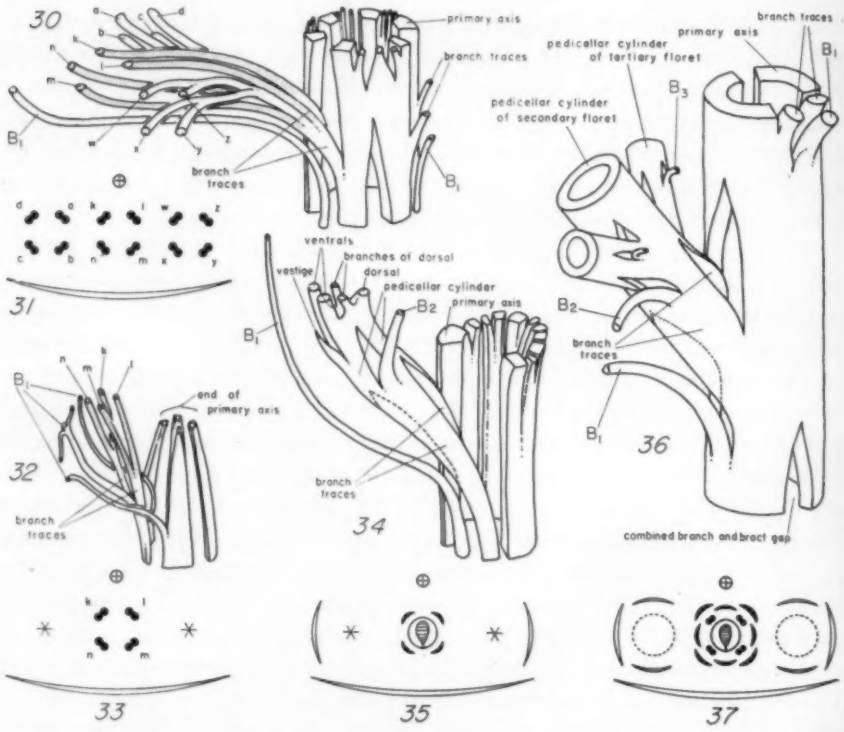
Of interest in indicating the effect of extreme crowding is the reduction in the staminate cymule of *Leitneria* shown in figures 9 and 10. Associated with this reduction is a marked modification of the vascular system of the cymule (fig. 29). The cymule is from the terminal portion of an ament. The two bracts above this had no flowers in their axils. The basic plan of the vascular system of the *Leitneria* cymule is much modified, embodying the complete loss of a vascular supply to the tertiary axes. Not only the vascular supplies to stamens *m* and *n* (as in fig. 24), but also the supplies to *k* and *l*, are derived by branching from the B_1 bundle. Fortunately there is a precedent already established in a less condensed portion of the inflorescence which permits the interpretation of two of these bundles as supplying stamens of the secondary floret. That the other two bundles may belong to this secondary floret is a logical conclusion, which is strengthened by the unusual supplementary vascular supply (*br*) to the primary bract. These two bundles (*br* and *br*) arise from the sides of the gap and topographically should be branch bundles, but their destination as part of the vascular system of the primary bract suggests that they have been modified from their original function. With the transference of the vascular supply of the median floral elements to the major median vascular bundle (B_1), the persistence of the branch bundles (*br* and *br*) is much to be wondered at and is apparently one of the vagaries to which the vascular system of the plant is subject. While these might be interpreted as corresponding to lateral bundles of the typical trilacunar supply of the foliage leaf (Sinnott, 1914), or even as secondary bract bundles, such contentions could hardly be maintained because the condition occurs in the most reduced part of the ament, while it is absent in less reduced regions.

SUMMARY OF INFLORESCENCE AND FLORAL MORPHOLOGY

The pistillate inflorescence.—This has its vascular system (fig. 34) but slightly modified from a normal condition (fig. 36). The primary bract bundle (B_1, fig. 34) is a clear-cut entity, as are the branch traces. The branch traces form a slightly dissected secondary axis cylinder from which secondary bract bundles (B_2) depart in the typical fashion.

The pistillate flower.—After the departure of the secondary bract bundles the four vascular bundles remaining (pedicellar cylinder, fig. 34) reorganize in the pedicel of the solitary pistillate flower to form the elements of the vascular supply to the simple pistil. There is some evi-

dence (vestige, fig. 34) to suggest that there may have been a second carpel in the gynoecium. Although the number of tepals varies, vascular tissue occurs in them but rarely, and even then there is no connection of this tissue with the main vascular system. Within the pistil there is evi-



Figs. 30–37. Relationship of the vascular systems of the staminate and pistillate cymules to a simpler condition. Fig. 30. Diagrammatic representation of portion of primary axis and staminate cymule showing least modified condition. Fig. 31. Floral diagram of cymule shown in preceding figure. Fig. 32. Diagrammatic representation of terminal portion of primary axis and staminate cymule showing most highly modified condition. Fig. 33. Floral diagram of cymule shown in preceding figure. Fig. 34. Diagrammatic representation of portion of primary axis and vascular supply to pistillate cymule. Fig. 35. Floral diagram of preceding figure. Fig. 36. Generalized diagram of hypothetical ancestral type, showing portion of primary axis and vascular supply to a single three-flowered cymule. Fig. 37. Floral diagram of preceding figure.

Abbreviations used: B_1, primary bract; B_2, secondary bract; *dr*, dorsal; *vn*, ventral; *tp*, tepal; *ves*, vestigial; *ped cyl*, pedicellar cylinder; *ov*, ovular bundle; *br*, branch trace.

dence that there were probably at least two ovules at an earlier stage in the phylogenetic development of the flower.

The staminate inflorescence.—This consists of three-flowered cymules spirally arranged on a lax primary axis, each cymule in the axil of a large primary bract. Secondary and tertiary bracts are absent externally, nor

has internal evidence been found of their former existence in the material studied. The vascular system in the less modified staminate cymules (fig. 30) is a combination of the independent supply to a primary bract (B_1) and the two bundles (branch traces, fig. 30) of the secondary axis. The secondary axis (stippled in fig. 30) gives off vascular tissue laterally which topographically belongs to the tertiary axes. The tissue of the secondary axis, after the departure of the tertiary vascular material, continues on in the median plane to supply the stamens (*k*, *l*, *m*, *n*, fig. 30) of the secondary floret. In slightly modified cymules (fig. 24) the supply to the secondary floret has become in part associated with the supply to the primary bract and in part with that of the tertiary axes. With extreme reduction (fig. 32), the supply to the secondary floret (*k*, *l*, *m*, *n*, fig. 32) has become completely associated with that of the primary bract (B_1), while the tertiary axes are completely lacking. The anomaly exists here of bundles which resemble branch bundles in origin, contributing secondarily to the vascularization of the primary bract.

The staminate flower.—The pedicellar system of the tertiary (or lateral) staminate flowers (shown free of stippling in fig. 30) is but the single bundle which branches after moving a short distance laterally to supply the stamens (*w*, *x*, *y*, *z*, fig. 30). The pedicellar vascular system of the secondary floret (shown stippled in fig. 30) consists of the vascular tissue left after the departure of the tertiary branches. This leaves four separate traces (*k*, *l*, *m*, *n*, fig. 30), each of which may supply a stamen. Neither external nor internal evidence of tepals or pistils was found in the staminate cymules. In spite of the absence of these landmarks the disposition of the vascular tissue leaves no doubt of the presence of three florets in the average cymule.

DISCUSSION

Interpretation of pistillate ament, inflorescence, and floret.—Telescoping in the pistillate material of *Leitneria* has not been as great as that found in some other amentiferous plants, a fact which has much simplified the study of its vascular system.

The presence of well-defined secondary bracts below the floret suggests, by analogy with the Betulaceae (Abbe, 1935), that tertiary florets were present in the phylogenetic history of the plant. This interpretation receives even stronger support from the evidence for the presence of tertiary florets in the staminate material.

Although the floret of *Leitneria* possesses a single, simple pistil, the presence of a vestigial bundle (fig. 22, *ves* 3) suggests that another carpel may have been present. Whether the ancestral pistil was simple or compound is a question that cannot be answered on the basis of our present knowledge. It is quite obvious that the ancestral form had a definitely

superior ovary. The presence of vestiges of vascular bundles within the ovary suggests that there were once several ovules present.

The range of variation in number of tepals described in the literature is not as great as that in our material. Here, they were sufficiently abundant and so arranged as to suggest two definite cycles. When present, the vascular supply of the tepals is so rudimentary that it apparently is no longer functional.

Interpretation of staminate ament, inflorescence, and floret.—The units of the staminate inflorescence have been generally interpreted as single flowers in the axils of the bracts. The vascular anatomy of the ament supports the fact that the primary bract is a simple morphological entity. In its axil there is definite vascular evidence of three flowers cymosely arranged. This is opposed to the former descriptions which allow but a single flower in the axil of each primary bract. In the simplest cases the vascular system of the secondary axis is distinct from that of the tertiary axes. In the upper portion of the ament there is more crowding of the stamens with a corresponding reduction in number in each floret. This condition, together with anastomoses of the vascular bundles, complicates the interpretation of the relationship of the florets and their vascular supplies. This phenomenon is not unusual, however, and parallels the condition found in similar inflorescences in the Betulaceae. In the latter group of plants the inflorescences are definitely reduced from three-flowered cyme-like units. There is similar evidence of the same thing occurring in the lower parts of the aments of *Leitneria*. In the extreme terminal portion of the staminate ament, however, there has been a complete transferral of the vascular tissue of the secondary axis to the midrib of the primary bract, an extreme expression of the tendency toward fusion. In this region of the ament there is also the unusual phenomenon of the primary bract receiving supplementary vascular tissue at its margin from bundles which had an origin characteristic of branch bundles, a condition which we are unable to explain.

In summary, our investigations of the staminate material of *Leitneria* make necessary a revision of the current idea concerning the organization of the units of the staminate aments. These units are composed of three flowers instead of a single flower in the axil of each primary bract.

THEORIES CONCERNING THE RELATIONSHIP OF LEITNERIA

The systematic treatment of *Leitneria* has been quite diverse. Because of its more or less catkin-like inflorescences, *Leitneria* has been frequently included in that heterogeneous assemblage, the "Amentiferae," or its equivalent (Chapman, 1860; Cas. DeCandolle, 1864; Eichler, 1878; Baillon, 1880; Bentham and Hooker, 1880; Engler, 1894; Wettstein, 1924; Engler and Gilg, 1924; Hutchinson, 1926). It has been placed in

the Dipterocarpaceae by van Tieghem (1886; 1891), but on an erroneous basis, as was pointed out by Heim (1891; 1892). Heim (1892) suggested as an alternative to van Tieghem's proposal, that *Leitneria* is related to the Hamamelidaceae. The latter view was sanctioned by Engler (1897) with the proviso that this would hold only if *Leitneria* were considered a reduced form. Hutchinson (1926) uses essentially this same interpretation in deriving *Leitneria* from the Rosales through the Hamamelidales. Hallier, at one time (1905) also considered *Leitneria* to be a member of the Hamamelidaceae, which, however, he derived from the Magnoliales. Later, he (Hallier, 1912) placed *Leitneria* in his "Terebinthacées" which he derived from the "Proberberideae" through the Rutaceae. Finally, Bessey (1915) placed *Leitneria* directly in the Ranales.

There is little beyond taxonomic convenience to recommend the lumping of *Leitneria* with the "Amentiferae." "Naturalness" has seldom been claimed for the group, except perhaps by Linnaeus (1751). No close relationship can be hypothecated between *Leitneria*, with its hypogynous flower, and the inferior-ovaried Fagaceae, Betulaceae, and Juglandaceae. Others of the "Amentiferae," although possessing superior ovaries, differ in other respects. Thus the Salicaceae, with the exception of two species of *Populus*, have ovules with but a single integument (Schnarf, 1931) in contrast to *Leitneria* which has the two integuments exceptionally well developed (Pfeiffer, 1912). The ovule of the Myricaceae not only differs from that of *Leitneria* in having but a single integument, but differs still further in the highly vascularized state of the integument, as well as of the nucellus. Furthermore, both the Salicaceae and the Myricaceae have syncarpous pistils, a type of gynoecium from which the single simple pistil of *Leitneria* is probably not derived. *Leitneria* differs in the same respect from the Garryaceae (in which the ovules are also provided with only one integument). The inflorescence of the Garryaceae with its opposite members is in this respect even more unlike *Leitneria*, with its spirally arranged members, than are the rest of the "Amentiferae" which have been mentioned up to this point. Such comparisons across the "genetic lines" could be continued within the variable limits of the "Amentiferae." It is, however, abundantly clear that *Leitneria* is as unlike the other "Amentiferae" as many of them are unlike one another.

By adopting a broad interpretation of orders (Engler and Gilg, 1924) the more recent suggestions concerning the relationship of *Leitneria* may be summarized as follows. It has been considered a member of the:

Ranales (Bessey, 1915).
Rosales (Heim, 1892; Engler, 1897; Hallier, 1905).
Geraniales (to include part of the "Terebinthacées" of Hallier, 1912).
Sapindales (to include the other part of the "Terebinthacées" of Hallier, 1912).
Parietales (van Tiegham, 1886, 1891).

An effort to evaluate these suggestions should be made on the basis of one of Bessey's (1915) well-known dicta. This is that "plant relationships are *up and down* the genetic lines, and these must constitute the framework of phylogenetic taxonomy." It is by no means a new concept, since Bessey in an earlier paper (1897) refers the gist of it to Asa Gray. An important corollary of this principle is that plants contemporary with each other cannot be related in a direct, linear fashion. They must go back to common ancestors even in cases of the closest relationships. It is of the greatest importance that phylogenetic theories which have developed in the past few decades be applied with this corollary in mind, although it has not been the usual practice to do so.

Furthermore, if an attempt is made to consider all of the available phylogenetic evidence, there should be put into practice another basic philosophy, which is often implied, but seldom expressed. Every feature of phylogenetic significance possessed by the plant or group of plants in question must be of such nature that it may reasonably be derived from that of the hypothecated ancestral form. The pitfalls in applying this working principle are numerous, nor can they be avoided, largely because of the absence of a clear paleobotanical record for the Angiosperms. Also, the larger the group of plants taken into consideration, the less "natural" it may be, and the more difficult it is to reach definite conclusions by the use of this working principle. It is unfortunate in this particular case that *Leitneria* is a monotypic form possessing so few distinctive features. The result is that it has been put into a number of different orders whose archetypes are notably similar in most respects.

It has been found useful to think in terms of archetypes of the five orders mentioned above, insofar as these archetypes may be reconstructed on the basis of current phylogenetic theories. The sum of the more primitive characteristics for each of these orders is considered to constitute the Archiranales, Archirosales, Archigeraniales, Archisapindales, and Archiparietales, respectively.

The archetypes of all five of these orders possess the primitively woody habit (Eames, 1911; Sinnott and Bailey, 1914b) from which *Leitneria*, which is a small tree, could well have been derived.

The primitively stipulate (Sinnott and Bailey, 1914a), simple and palmately veined (Sinnott and Bailey, 1915) type of leaf whose vascular supply is trilacunar in origin (Sinnott, 1914) characterizes the archetype of each of the five orders. From this type of leaf it is easy to derive the simple, pinnately veined, exstipulate leaf of *Leitneria* with its trilacunar origin of the leaf traces.

Either the very primitive solitary flower (Parkin, 1914; Zimmermann, 1935) or relatively simple inflorescences occur in the archetypes of the

five orders. Such certainly precede the highly modified type of inflorescence found in *Leitneria*.

The much modified type of vessel member in *Leitneria* (Type IV, Bailey and Tupper, 1918) with its simple perforation plate and alternate pit arrangement on the side walls is considered more advanced than the absence of vessels in the Archiranales, the Type I vessel member in the Archirosales, Archisapindales, and Archiparietales, or the Type III vessel member of the Archigeraniales (Bailey and Tupper, 1918).

The secondary xylem of *Leitneria* (Heim, 1892; Trelease, 1895; verified by the writers) is further highly modified in having vessels arranged in radial or diagonal pore chains, in contrast with which Frost (1930) considers the diffuse porous type more primitive. The bulk of the xylem is composed of thin-walled elements with minute pits whose apertures are relatively elongate, and of some septate elements; while the primitive type of tracheary element is considered to be simple rather than septate and to have large scalariform pits (Frost, 1930). The xylem parenchyma in *Leitneria* is terminal, while diffuse parenchyma is considered more primitive (Jeffrey, 1917). The xylem rays are mostly uniseriate and heterogeneous, considered an advanced condition by Kribs (1935). So advanced is the secondary xylem of *Leitneria* in these various respects that there would seem little difficulty in deriving it from the archetypes of any of the five orders in question.

We tentatively interpret the flower of the immediate ancestor of *Leitneria* as bisexual, with a perianth composed of two cycles, at least one cycle of stamens, and perhaps a several-carpelled gynoecium. While we feel that the ancestral gynoecium was probably apocarpous, we recognize the possibility of its origin from a syncarpous one (by analogy, for instance with the tendencies in the Valerianaceae and Dipsacaceae), although there is no internal evidence to support the latter view. The floral organization of the archetypes of the five orders is either spiral or spirocyclic, and apocarpous. Tentatively any of these combinations may be considered as suitable ancestral conditions for the much reduced flowers of *Leitneria*.

The anatropous position of the ovule with the micropyle turned away from the placenta in *Leitneria* appears to provide a diagnostic feature which would serve to exclude the Archisapindales, since the latter are characterized by the reverse orientation of the micropyle when the ovule is anatropous. The other four orders may well have had a type of ovule orientation from which that of *Leitneria* could have been more readily derived.

Two extremely well-developed integuments are present in the ovule of *Leitneria*, a condition which is also to be found in the archetypes of the five orders.

The eight-nucleate embryo-sac with its ephemeral antipodals develops from a megaspore in the typical manner in *Leitneria*. The megaspore is one of four derived from a megaspore mother cell, which in turn is derived from a single archesporial cell (Pfeiffer, 1912). There is general agreement that the eight-nucleate type of embryo-sac is primitive (Schürhoff, 1926; Schnarf, 1931, 1936), but its wide distribution throughout the Angiosperms, including the archetypes of the five orders, makes it of no diagnostic significance. The relatively primitive condition of the origin of the embryo-sac from a megaspore rather than from a megaspore mother cell is common to all five of the orders being considered.

Whether the cellular type (Schürhoff, 1926) or the nuclear type (Schnarf, 1931) of endosperm is to be considered the more primitive, the presence of the nuclear type in *Leitneria* (Pfeiffer, 1912) as well as in all five of the orders renders this category of information useless.

Leitneria is crassinucellate (Pfeiffer, 1912), a condition which is considered more primitive than the tenuinucellate (Schnarf, 1936). But the archetypes of the five orders are also uniformly crassinucellate.

The large size of the suspensor in *Leitneria* (Pfeiffer, 1912) is a primitive characteristic which is not shared by the archetypes of the Sapindales and Parietales, but does characterize the archetypes of the Ranales, Rosales, and Geraniales. Except for the fact that our knowledge of the details of embryology in many families is limited to but a single species each, this might be considered an important basis for the exclusion of the Archisapindales and Archiparietales from further consideration. As it is, it provides merely a tentative reason for excluding the archetypes of these two orders as potential ancestral forms of *Leitneria*.

The large number of cells ("hundreds") in the embryo of *Leitneria* (Pfeiffer, 1912) also suggests the origin of *Leitneria* from more primitive archetypes.

The chromosome number and the development of the male gametophyte in *Leitneria* are both unfortunately unknown as far as we are aware.

Thus there is little gained of a positive nature in attempting to decide whether *Leitneria* is more likely to have been derived from the Archiranales, Archirosales, Archigeraniales, Archisapindales, or Archiparietales. The orientation of the ovule, the massive suspensor, and the nature of the young embryo, and possibly the gynoecium serve provisionally to exclude the Archisapindales from further consideration. Their slender suspensor, less primitive embryo, and possibly the structure of the gynoecium, seem also to eliminate the Archiparietales. There remain the archetypes of the

Ranales, Rosales, and Geraniales between which there is very little choice. The Ranales might be excluded because of the great changes which would have to be undergone by *Leitneria* to derive it from the Archiranalean type. This tentatively leaves the Rosales (including the Hamamelidaceae) or the Geraniales as potentially logical orders in which to leave the Leitneriaceae.

Further information concerning the Leitneriaceae (especially chromosome number and morphology, and the development of the male gametophyte) as well as a better co-ordination of the phylogenetic data for other families is needed. Perhaps then *Leitneria* may be placed with somewhat more certainty.

SUMMARY

1. The pistillate flower of *Leitneria* is composed of a single, simple, uniovulate pistil surrounded at the base with a perigon composed of three to eight diminutive tepals.

2. There is vascular evidence in the pistillate flowers which suggests the former existence of a larger number of ovules and carpels. We are of the opinion that the gynoecium is derived from an apocarpous ancestral form.

3. The pistillate flowers are solitary in the axils of primary bracts, each of which is accompanied by two secondary bracts. The pistillate inflorescence is a relatively few-flowered spike.

4. The staminate flower is composed of one to four stamens unaccompanied by tepals.

5. There is vascular evidence that three flowers occur in the axil of each primary bract of the staminate inflorescence. No secondary bracts were observed. The staminate inflorescence is a many-flowered compound ament.

6. The possibility of the origin of *Leitneria* from the archetypes of the Ranales, Rosales, Geraniales, Sapindales, and Parietales (as suggested by various writers) is surveyed. It is tentatively concluded that the Archiranales, Archisapindales, and Archiparietales would be less likely ancestral forms than the Archirosales or Archigeraniales. The Leitneriaceae is left in either the Rosales or Geraniales, and the need for more diagnostic evidence is stressed.

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Studies in the Crassulaceae: Villadia, Altamiranoa and Thompsonella

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Two recent authors, Baehni (1937) and Walther (1938), have published independently on the status of the generic names, *Villadia* and *Altamiranoa*. Essentially opposite conclusions were reached concerning the nomenclature, although both writers agreed that the species in these two genera proposed by Rose (1903) really belong together in the same genus. Baehni chose for the aggregate genus the name which has page priority, i.e., *Villadia;* Walther, by identifying the type species of *Villadia* with *Thompsonella minutiflora*, restricted *Villadia* to the two species of the former *Thompsonella* and employed *Altamiranoa* for the aggregate genus, resulting from the fusion of the rest of the species of *Villadia* with the species of *Altamiranoa* as defined by Rose.

Faced with the need of reaching a conclusion concerning which of these authors to follow, I have reviewed the available evidence. At first reading, the argument of Walther appeared entirely satisfactory and it seemed reasonable to adopt his conclusions. Further study, however, indicated certain difficulties which could not be ignored. Walther republished the original illustration of the type of *Thompsonella minutiflora* (Rose) Britton and Rose. He also reproduced a photograph of the type specimen of *Cotyledon parviflora* Hemsley, on which *Villadia* is based, from the Kew Herbarium in England. These illustrations were placed side by side by him for comparative purposes, and were claimed to represent plants of the same species. Casual observation of Walther's plate indicated this conclusion to me, but close investigation revealed differences in the orientation of the top of the inflorescence, relation of the flowers to the bracts, number and shape of cauline leaves, and presence or absence of rosette leaves. When thirteen herbarium specimens exactly matching the illustration of the type of *Cotyledon parviflora* were compared with four identical with Rose's *Thompsonella minutiflora*, still further differences were evident which could not be made out from the illustrations. The two kinds of plants were abundantly different, as is shown in the following table, in which the distinguishing characters are set forth.

Cotyledon parviflora	*Thompsonella minutiflora*
1. Petals connate for ⅓ their length.	Petals connate for ⅛ of their length.
2. Sepals glandular roughened.	Sepals smooth.
3. Flowers strictly axillary.	Flowers inserted somewhat above the subtending bracts.

4. Cauline leaves linear, terete, acute, numerous (±36).	Cauline leaves thick, ovate-oblong, few (±5).
5. Basal rosette leaves absent. (Careful examination of plants with roots failed to reveal evidence that there had been rosette leaves which had disappeared prior to collection.)	Basal rosette leaves present.
6. Flowering stem somewhat curved or nodding at tip.	Flowering stem erect.
7. Stems and leaves green.	Stems and leaves suffused with purple.

In view of this evidence, Walther's conclusions seem quite unsatisfactory and untenable, and it is necessary to reject the fourteen new specific combinations which were made by him on a basis of those conclusions. Since references were not supplied to the previously published descriptions of the species, none of these new combinations are truly valid anyway, but they are now in print to cause confusion.

For those who may wish to check the differences between the two species mentioned and to test the correctness of the above statements, I cite the specimens on which my conclusions are based. In the citations, BH represents Bailey Hortorium and NY, New York Botanical Garden.

Villadia parviflora (Hemsley) Rose. ARIZONA: San Francisco Mts., 1904, *C*——— (name on label is not clear) *and Lloyd,* specimens flowered at NY, July, 1905, *21179* (NY). MEXICO. Hidalgo: near El Salto, September 16, 1903, *J. N. Rose & J. H. Painter 820 and 7116* (NY). San Luis Potosi: 22° N. lat., 6,000–8,000 ft., 1878, *C. C. Parry and E. Palmer 238* (NY); from the valley, *J. G. Schaffner 383* (NY). Tamaulipas: valley near Tula, *C. G. Pringle 9637* (NY). Zacatecas: Zacatecas, *C. A. Purpus* (*J. N. Rose 931*) (NY). Valley of Mexico, *J. N. Rose 19184* (NY); *L. H. MacDaniels 770* (BH).

Thompsonella minutiflora (Rose) Britton & Rose. Mexico. Puebla: Tehuacan, *J. N. Rose 25662* (NY), *C. A. Purpus 19985* (NY), *M. B. Halsted* (NY).

Baehni rightfully did not confuse his discussion of *Villadia* with the *Thompsonella* problem. Under *Villadia,* he made new combinations for eight species of *Altamiranoa* and one species of *Sedum.* So far as I have had opportunity to check, these appear justifiable, particularly since the characters for separation of *Altamiranoa* and *Villadia* seem not of generic importance.

Nine specific names still remain in the now abandoned *Altamiranoa.* I am prepared to transfer one of these to *Villadia,* but feel that it is both unwise and unnecessary to publish new combinations for the others until after critical study of actual specimens to determine the specific validity of each of the entities. The one new combination that I make below is

necessary because the plant is in cultivation and requires a definite designation at once. So far as known to me, the other species concerned are not in the horticultural trade and specimens have not been available to me.

Thompsonella appears distinct from *Villadia*, but I am in no position now to consider its relation to *Echeveria*. My casual tendency is to follow Berger, who reduced it to a section of *Echeveria*, since the plants have the appearance of that genus, but I have not given careful study to the matter.

As now considered, *Villadia* Rose (*sensu latiore*) contains about twenty-five species and is capable of division into two sections, EUVILLADIA (*Villadia* Rose, Bull. N. Y. Bot. Gard. 3: 3. 1903.) and **Altamiranoa** (Rose) n. stat. (*Altamiranoa* Rose, Bull. N. Y. Bot. Gard. 3: 31. 1903.). The genus includes a group of species which are intermediate in character between *Sedum* and *Echeveria*. It is characterized by the petals somewhat connate at the base, the inflorescence terminal, the flowers small, and the absence of rosette leaves. *Echeveria* has rosette leaves, large flowers, and the inflorescence borne laterally. There are also various other minor differences which serve to distinguish these genera, but the principal ones are those given.

The Section ALTAMIRANOA differs from EUVILLADIA in having the flowers borne on one-sided racemes or cymes. In the typical section the flowers are arranged in equilateral racemes, spikes, or compact panicles. Since, for consistency, it would be necessary to divide *Echeveria* into two genera likewise, if this difference in the inflorescences were employed here as basis for generic segregation, also since it is known that this character is subject to great variation, as already remarked by both Baehni and Walther, the placing together of *Altamiranoa* and *Villadia* seems logical. Besides the character afforded by the inflorescence, the species of the section *Altamiranoa* usually have more slender roots than do those of *Euvilladia*.

As now interpreted, the section ALTAMIRANOA contains ten species. Several others will probably be shown in the future also to belong here. The species at present placed in the section are:

Villadia andina (Ball.) Baehni and Macbride, Candollea 7: 285. 1937.

Villadia Batesii (Hemsl.) Baehni and Macbride, Candollea 7: 285. 1937.

Villadia Berillonana (Hamet) Baehni and Macbride, Candollea 7: 285. 1937.

Villadia Dielsii Baehni and Macbride (*Cotyledon stricta* Diels.), Candollea 7: 285. 1937.

Villadia Dyvrandae (Hamet) Baehni and Macbride, Candollea 7: 286. 1937.

Villadia elongata (Rose) comb. nov. (*Altamiranoa elongata* Rose, Bull. N. Y. Bot. Gard. 3: 31. 1903).

Villadia Grandyi (Hamet) Baehni and Macbride, Candollea **7**: 286. 1937.
Villadia imbricata (Diels) Baehni and Macbride, Candollea **7**: 286. 1937.
Villadia incarnum (Ball) Baehni and Macbride, Candollea **7**: 286. 1937.
Villadia virgata (Diels) Baehni and Macbride, Candollea **7**: 286. 1937.
Villadia Weberbaueri (Diels) Baehni and Macbride, Candollea **7**: 286. 1937.

The eight remaining species of *Altamiranoa*, some of which may also be removed to *Villadia* as a result of further study, are:

Altamiranoa alpina Fröd. Concerning this, Fröderström (1935) commented: "It is apparently a distinct species but may also be but an alpine reduced form of *A. Batesii*."

Altamiranoa decipiens (Baker) Fröd. Without specimens, I am decidedly uncertain about the proper status of this.

Altamiranoa Galeottiana Rose. According to Rose (1903) this is known only from the type locality. It should be studied very carefully before subjecting it to further nomenclatorial innovations.

Altamiranoa Jurgensii (Hemsley) Rose. This is known only from the type specimens. Fröderström (1935) made it a variety of *Altamiranoa elongata*, but without specimens, I can reach no satisfactory conclusions.

Altamiranoa mexicana (Schlect.) Rose. According to Rose this is known only from the type locality. Fröderström (1935) wrote: "A doubtful species, unknown to me."

Altamiranoa necaxana Fröd. In his original decription, Fröderström (1935) remarked that this is closely allied to *A. elongata* and perhaps only a glabrous variety of that from a less extreme region.

Altamiranoa ramulosa Fröd. This was based on Pringle's collection no. 4287. It is not clear to me why it is not an extreme variation of *Villadia Batesii*.

Altamiranoa scopulina Rose. Apparently known from the type collection only and little understood.

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Plant Responses to Carcinogenic agents and Growth Substances; their relation to Crown Gall and Cancer [1]

MICHAEL LEVINE

(WITH 34 FIGURES)

The isolation of *Bacterium tumefaciens* from wart-like growths on the stems of the Paris daisy, *Chrysanthemum frutescens*, and the production of similar overgrowths by inoculation with bacteria on a large number of species of plants, has led to the conception that these localized growths are analogous to malignant neoplasia of animals. The work of Smith (1911) who sponsored this view is well known and little need be said except to recapitulate briefly the salient features upon which these contentions were based. Smith held the view that crown gall is a malignant plant disease consisting of localized proliferation of the host cells induced by *B. tumefaciens*. The new mass of disoriented cells, at times, invaded the healthy host tissue and interfered with its normal function. The effects on the plant so infected was to cause it to become dwarfed, to lack power to form flowers and fruit, and finally to cause death.

A critical study of this disease in relation to animal cancer has been in progress in this laboratory for more than twenty years. It has been contended by the present writer (Levine, 1931–1936) that crown gall is not analogous to animal cancer. The fundamental attributes of animal cancer are dependent upon the inherent characteristics of animals. The multiplicity of cancer forms found in the animal have no analogy in the simple overgrowths found on the plant. In the absence of blood and lymph systems, metastases cannot occur in plants. The invasive character of the plant overgrowth occurs principally under certain experimental conditions. The dwarfing and death of the plant are dependent upon the site of the overgrowth. In most cases death of the plant is secondary to mechanical destruction of supporting tissues.

Cytologically, crown gall and animal neoplasia have one property in common. In both types of abnormal growth, the mass of new tissue is increased by rapid division of the stimulated or rejuvenated peripheral cells. The types of division in animal cancer are aberrant. Cells with atypical numbers of chromosomes are found which result from chromosome division without intervention of the spindle fiber mechanism. In plants, the normal process of division is similar to those found in rapidly dividing embryonic cells. Polyploid cells occur in the overgrowths due to

[1] Read before Section VI of the Third International Congress for Microbiology in New York City.

repeated nuclear division without cell division. The tumor giant cells in malignant animal cancer have no known origin. Malignant animal cancer is characterized by continuous growth of the new tissue with variation in the tempo of proliferation. In plants the continuity of the overgrowth is in a larger measure determined by the environmental conditions. Generally, plant overgrowths on annuals are short-lived. The tissue matures, the cells become old and differentiate forming woody structures; death follows. On perennials, subjected to seasonal changes, the overgrowths die, although the stem or branch upon which they are produced lives. Reinfection occurs with resumption of growth in the following growing season. In the case of sheltered succulent perennials, the new growths may live for a longer period, but ultimately their tissues undergo differentiation, become old, corky or leathery, and die.

Animal tumors are known to regress; the mechanism which makes this possible in the animal is entirely lacking in the plant. A wart-like overgrowth on a plant regresses by drying and shriveling. Obviously the cells of the overgrowth are not carried away by phagocytes. Yet crown gall disease is nevertheless a neoplastic disease. It undoubtedly belongs in the category of tumor diseases although its analogy to animal or human cancer is not apparent. It now appears that cancer of man and animal may arise from many causes. Experimentally, the production of cancer in animals by chemical means started with the induction of tar tumors of rabbits (Yamagiwa and Ichikawa, 1916). The production of active carcinogenic tars (Kennaway, 1924), the isolation and synthesis of 3, 4-benzpyrene (Cook, Hewett, and Hieger, 1933), the preparation of methylcholanthrene, the synthesis of 1, 2, 5, 6-dibenzanthracene (Clar, 1929), and finally the production of more than 40 chemical substances, synthesized by Fieser (1938) and his associates in America, and by Cook (1937) and his collaborators in England, have been shown to possess carcinogenic properties of greater or less potency. Styryl 430, radium, thorotrast, unrelated chemical agents, are known to produce cancer in man and animal. Endocrine products such as oestrin play an important rôle in cancer production. Cancer induced by these chemical agents are malignant growths and present cellular and clinical pictures like spontaneous neoplasia known to man and animal.

The chemicals applied locally to plants have been productive of overgrowth responses which have been described as tumors with the implication that these local excrescences may be in some way associated with malignant growths of animals.

It has been hoped that with the discovery of chemical agents as the etiological factors in cancer of animal and man, that these substances would likewise induce malignant overgrowths on plants. The early results of

application of chemical agents on plants has been reviewed (Levine, 1934). Komuro (1932) speaks of "phytoteertumors" induced on *Pisum sativum* and *Vicia faba* with tar solutions. The cytological phenomena described in the roots of these plants are suggestive of the cellular phenomena found in cancer. Havas (1939) stresses responses of plants and animals to various chemical agents as analogous. Zimmerman (1937) and collaborator, Wilcoxon (1935) showed that the application of a number of synthetic compounds,[2] most important of which is indoleacetic acid, applied to any part of a plant induces epinasty, swellings, proliferations, and roots, at the treated area. Horticulturally, these findings appear to be of economic importance.

Brown and Gardner (1936) studied the effects of 0.4 per cent suspension of indoleacetic acid and indolepropionic acid in lanolin on the bean, tomato, and sunflower. These plants responded by producing definite overgrowths. *Bryophyllum* and *Kalanchoë* produced roots only. Galls were also produced by a growth substance extracted from *B. tumefaciens* growing in media containing tryptophane. Kraus, Brown, and Hamner (1936) studied the histological effects of 0.6 per cent indoleacetic acid in lanolin on the red kidney bean grown under greenhouse conditions. They concluded that the histological development following the application of indoleacetic acid closely resembled many of those associated with crown galls produced by *B. tumefaciens*. Hamner and Kraus (1937), in a further study of the effects of a paste of indoleacetic acid (3 per cent) in lanolin to decapitated bean plants, found that these plants produce large vascular overgrowths, many of which continue to develop for a period of six months and attain a diameter of 2 cm. or more. Application of indolebutyric acid or α-naphthaleneacetic acid resulted in similar tumors on the bean plant. Roots are associated with the development of these tumors. Partially mature bean pods, when injured and treated with these agents, produce comparatively large overgrowths. Harrison's (1937) study on *Iresine Lindenii*, and Hamner's (1938) investigation of *Mirabilis Jalapa* gave results comparatively similar to those obtained with indoleacetic acid on bean plants. Beal's (1938) study of the monocotyledon *Lilium philippinensi formosanum*, *L. longiflorum*, and *L. Harrisii* are of interest since the monocotyledonous plants are resistant to the crown gall organism. The application of indoleacetic acid produces, according to Beal, two distinct types of reactions. The first two species of *Lilium* produce roots while *L. Harrisii* produces buds on application of heteroauxin. The roots formed were normally vascularized and appear to arise from the paren-

[2] α—naphthaleneacetic acid, β—naphthaleneacetic acid, acenaphthyl-5-acetic acid, indolebutyric acid, indoleacetic acid, indolepropionic acid, phenylacetic acid, and α—naphthylacetonitril.

chyma about the outer bundles. The buds arise in the cells of the epidermis and cortex in the vicinity of the leaf axil. The cytological study shows normal structures and normal cell divisions. No tumors or overgrowths were produced on these lilies.

Link, Wilcox, and Link (1937[1, 2]) made a comparative study of the effects of the crown gall organism, the extract of the organism, indoleacetic acid, and wounding on the bean and tomato plants. They contended that native growth substances can be augmented or replaced by synthetic growth substances or heteroauxin. These substances at different concentrations and amounts may produce tumors as well as those reactions characteristic of injury. Link believes that galls are possibly incited by *Bacterium tumefaciens* through heteroauxin in conjunction with other chemical agents, for *B. tumefaciens* produces indoleacetic acid when grown in media containing tryptophane. Bending of hypocotyls of bean seedlings was induced within several hours by bacterial extracts, thickening of the hypocotyls, and finally the appearance of whitish tumors adjacent to the region of application were reported. More pronounced effects were produced by heteroauxin. The effects of tryptophane (indole-α-aminopropionic acid) has not been studied. Link and Eggers' (1938) study of the hypocotyls of flax seedlings led them to believe that indoleacetic acid at varying concentrations inhibits bud initiation, but induces apical tumors, while lower concentrations retarded and diminished bud formation and decreased tumor formation.

Berthelot and Amoureux (1937) studied the effects of 1, 2, 5, 6-dibenzanthracene, benzpyrene, indoleacetic acid as well as folliculin and allantoin on the stem of a small number of sunflower seedlings. Folliculin and benzpyrene treated stems yielded reactions, while their plants died after treatment with indoleacetic acid. In their later report (1938), they contend that indoleacetic acid reactions were analogous to crown galls obtained with *B. tumefaciens* inoculation. They claim that the crown gall organism produces indoleacetic acid in the presence of tryptophane.

Riker and his associates (1938[1, 2]) (1939) made comparisons between the physiological responses induced by inoculation with *B. tumefaciens* and those called forth by treatments with growth substances. The chemical composition of galls as contrasted with the adjacent tissue was also studied. Riker (1939) stresses the point that the great diversity of substances which call forth reactions in plants are not as important as the irritation or injury induced by them. He denies the importance of indoleacetic acid in crown gall formation and suggests that the factors which start the gall may be different from those which maintain its cellular proliferation.

The present study is a continuation of the work started a number of years ago (Levine, 1934, 1936, 1937) to induce tumors in plants by carcinogenic agents and to contrast the reactions with those induced by growth substances and by *B. tumefaciens*. Stress is laid principally on the histological structure of the heteroauxin overgrowth which consist of abortive organoids of parenchymatous tissue with feeble proliferating power. These overgrowths are short-lived and do not possess the power to grow like crown gall tissue. As biological entities in the category of neoplastic diseases, it is contended, that these new growths belong in the scale lower than crown gall. Nevertheless, indoleacetic acid under certain conditions produces small, nodular masses which present histological pictures similar to those observed in crown gall tissue. Their longevity, their power of continued proliferation, has not been found identical with crown gall tissue or malignant cancer of animals and man.

METHODS

The following report deals with a gross and histological study of the effects of 1, 2, 5, 6-dibenzanthracene, methylcholanthrene, 3, 4-benzpyrene, indoleacetic acid, nicotinic acid hydrochloride, sucrose, scharlach red, vitamin B_1, extracted auxin of broccoli flowers, oat leaves, and cultures of *B. tumefaciens*, *P. rhizogenes*, *P. fasciens*, and the woolly knot organisms. Twenty-one species of plants were used upon which more than 1300 treatments were made. Most of the species of plants used in these experiments had been previously studied. The species principally used in this series are *Kalanchoë Daigremontiana* Hamet and Perrier, *Bryophyllum calycinum* Salisbury and *Brassica oleracea botrytis*. Further data on *Nicotiana glauca*, sunflower, and red kidney bean are presented.

In these studies attempts were made to increase the initially stimulated growths with extracted auxin. The application of growth stimulating substances like indoleacetic acid, heteroauxin, and scharlach red were followed by treatments of extracted auxin from broccoli or oat leaves, or with crystalline B_1. These substances were suspended in hydrous lanolin (1 per cent to 3 per cent) and applied with a glass rod. Scharlach red was dissolved in ether which was applied to the area as a paint. The stems of the young plants were treated after decapitation frequently followed by pricking the cut surface with a sterile needle. The soft tissues of the stem, in many instances, were merely injured by piercing with a sterile needle. Control plants were injured in a similar fashion and were treated with ether or lanolin. Cultures of a virulent strain of *B. tumefaciens* were also used as checks on the capacity of plants to respond to the crown gall organism. Tissues at various intervals were removed and fixed in Bouin's solution, and Flemming's weaker solution. The tissues were imbed-

ded in paraffin and sectioned 7½μ to 15μ. Woody tissues which resisted sectioning were kept in the paraffin oven at 52° for varying lengths of time. Sections were stained with Flemming's triple stain and Heidenhain's iron alum haematoxylin.

KALANCHOË

Bacterium tumefaciens.—Young succulent plants of *Kalanchoë Daigremontiana* Hamet et Perrier when decapitated and inoculated with a virulent strain of *B. tumefaciens* produce on the area treated, a small nodular overgrowth. In 45 to 50 days rudimentary leaves arise from the upper surface of the crown gall, and an abundance of roots are formed on its lower surface and on the adjacent tissue of the stem. Notches of the leaves inoculated with the crown gall organism form globular masses of crown gall tissue with no embryonic shoots, leaves, or roots as previously shown for *Bryophyllum.* For purposes of comparison, crown galls were studied over a period of more than a year. Frequent photographs were made during this time to record the changes which occurred.

Scharlach red.—The effects of scharlach red in ether has already been reported (Levine, 1939). Here it is necessary to add only the results of further study on the development of these growths, a small number of which behaved like those inoculated with *B. tumefaciens.* The overgrowth shown in figure 1 was photographed about a year after treatment. The stem on which this gall developed began to dry while the apical leaves persisted. The gall is soft, leathery; the leafy protuberances and roots are apparently dead. Microscopic study of parts of the gall six months after the treatments were made, showed evidence of healing or regeneration. The white tissue of the gall became covered with a greenish epidermis which nearly covered the exposed surface. A microscopic examination of the tissue showed an abundance of normally organized stems and roots as in figure 2. Under high magnification typical crown gall-like tissue was observed; woody elements were irregularly distributed through masses of parenchymatous tissue as shown in figure 3. A more detailed study of the softer tissues is shown in figure 4. Here uninucleate and binucleate cells are of frequent occurrence. Isolated and disoriented clusters of xylem tubes are shown. Surrounding this mass of active tissue are parenchyma cells of larger dimension, many of which show an abundance of granular substances.

Another favorable response on a *Kalanchoë* to treatment with scharlach red dissolved in ether, was much slower in making its appearance. There was little reaction in the treated area for over a period of a month; in the interim, however, the decapitated stem regenerated a new shoot.

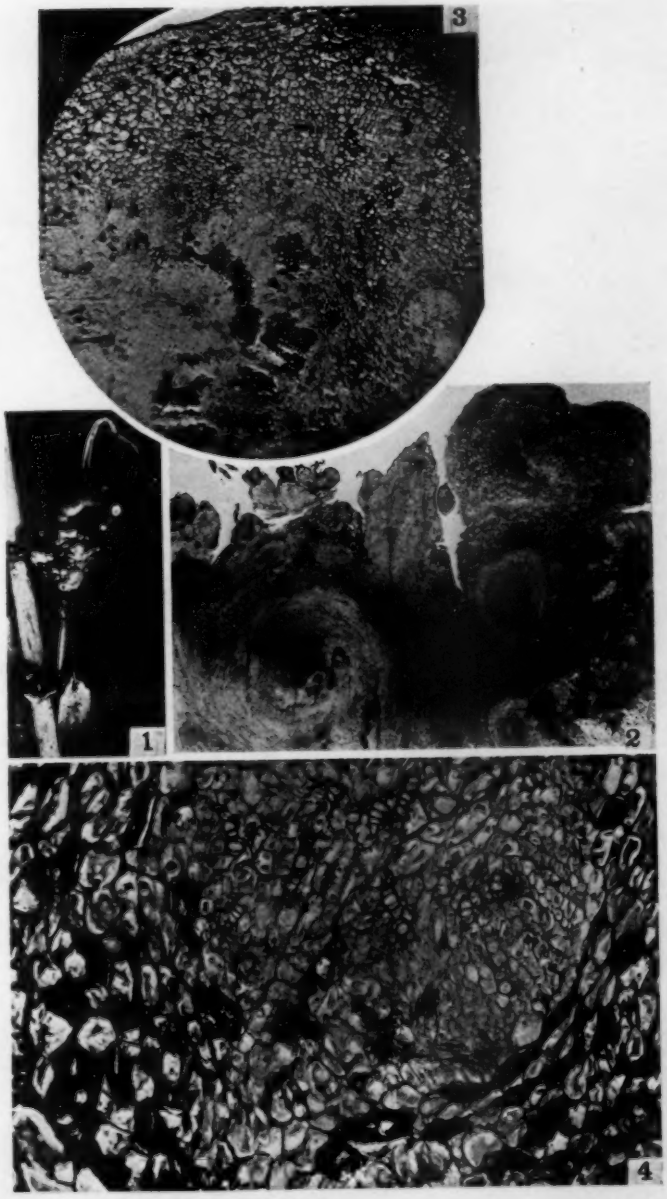


Fig. 1. Crown gall-like structure on *Kalanchoë Daigremontiana* treated with 1% scharlach red suspended in ether, one year after treatment. ×¾.

Fig. 2. Section through the overgrowth showing organoids, six months after treatment. ×7½.

Fig. 3. Portion of tissue shown in figure 2. ×30.

Fig. 4. Portion of the same tissue under higher magnification. ×200.

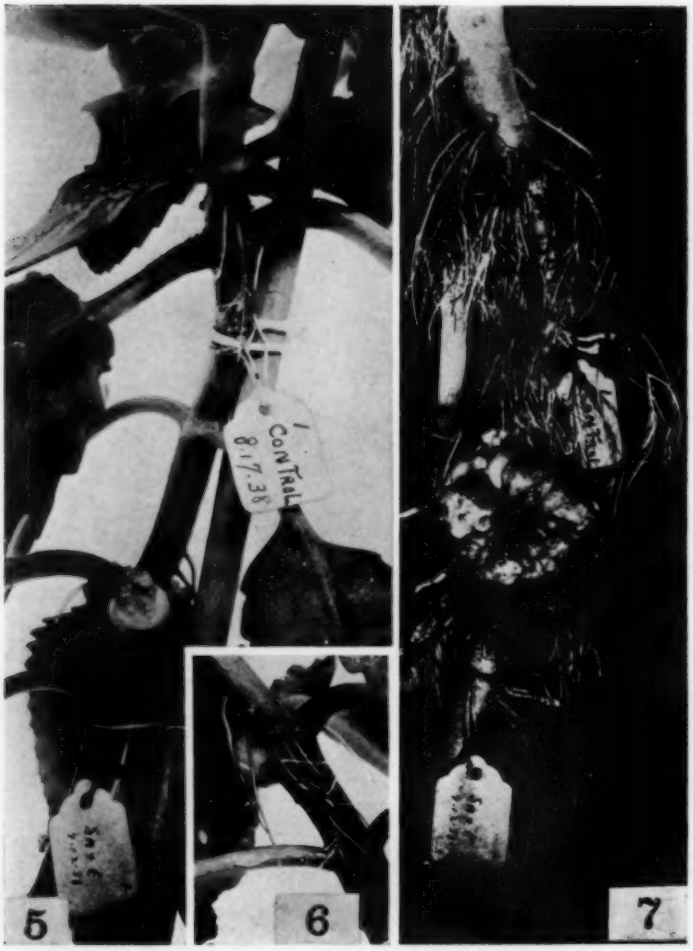


Fig. 5. Another *K. Daigremontiana* with small flattened globular mass with irregular greenish protuberances, six months after treatment with 2% scharlach red in ether. Note also root formation on control treated five months previously. ×¾.

Fig. 6. Same stem showing site of roots and discrete nature of the overgrowth. ×¾.

Fig. 7. Stem shown in figure 6 one year after treatment. ×¾.

Six months after the treatment, a flattened, globular, pale greenish mass appeared which at this time was nearly ½ cm. in diameter. This was surrounded by green protuberances which appeared to be undifferentiated leaf-like structures as shown in figure 5. A few roots appear to arise from the lower surface of the gall (fig. 6). The nodes of the plant now showed long roots from which secondary roots had grown. The control treatment, which consisted of an application of lanolin after injury, showed

little effect after a month. Six months later the surface of the control area turned black, but from the healthy, internodal tissue above, long roots appeared.

The overgrowth was carefully inspected at frequent intervals and a year after treatment necrosis of the upper surface of the gall appeared as shown in figure 7. No leafy structures were finally developed. Growth of the periphery of the gall occurred only. Sections of this tissue were not

Fig. 8. *K. Daigremontiana* in which the apical node has been decapitated and the internode treated with 3% indoleacetic acid in lanolin, two and a half months previously. ×¾.

Fig. 9. Section of treated area shown in figure 8. ×30.

Fig. 10. Portion of figure 9 enlarged showing normal cortical cells from which hyperplastic cells appear to arise. ×200.

examined microscopically. Note the abundance of roots in this treated area as well as the nodes above the gall. This type of gall is not characteristic of this species for crown galls on stems of the plant invariably produce leafy structures. Current studies on *Kalanchoë* under somewhat different conditions have shown, 50 days after treatment with 2 per cent scharlach red in ether, no roots but regeneration of the decapitated stem with slight protuberances about the treated area.

Indoleacetic acid, heteroauxin.—The effects of indoleacetic acid have been studied on decapitated and injured stems of Kalanchoë. Figure 8 shows a plant decapitated and treated with a 3 per cent suspension of indoleacetic acid in lanolin. The remnant of the decapitated internode is now surmounted by small nodular masses which are characteristic of the responses reported by various workers. On microscopic examination, this tissue presents undeniable evidence of rapidly proliferating cells, not

unlike those found in the active tissue of crown gall. Here there is no evidence of roots so typical of the plants injured by needle pricks and treated with indoleacetic acid. Figure 9 shows a low power view of a section of the apical portion of this overgrowth. The major part of the tissue consists of mature, well-differentiated, parenchymatous cells. Bordering this tissue and lying on its periphery is an irregular layer of tissue consisting of embryonic-like proliferating cells, the histological nature of which is shown more clearly in figure 10. In this figure one of a number of serial sections is shown, made through the center of a protuberance. There appears to be no connection with the meristematic tissue of the host. The cells are disoriented, of various sizes, and show from one to two nuclei. Fibrovascular elements have developed, haphazardly, through the actively growing tissue of the mass. This histological structure resembles closely those described for crown gall. Should one apply the methods of tumor diagnosis employed by the animal pathologist, this tissue would be classified as crown gall. However, the clinical pictures of crown gall and those produced by indoleacetic acid are entirely different. Perhaps the most salient feature is the failure of indoleacetic acid and other growth substances studied, to endow the new cells with prolonged power to proliferate.

The decapitated pricked stems of *Kalanchoë* followed by application of 3 per cent indoleacetic acid in lanolin is followed in seven days by the appearance of roots along the internode, even though the surface of the decapitated internode only was treated. In figure 11 a plant treated twelve days previously with the heteroauxin is shown. The treated portion of the stem becomes cracked, nodules appear which rapidly degenerate or dry up.

Carcinogenic Hydrocarbons.—In contrast with the effect induced by the indoleacetic acid, the response of the Kalanchoë to the carcinogenic hydrocarbons was different. The dibenzanthracene, however, as already shown (Levine, 1939) behaved much like the indoleacetic acid in that long, branching roots are found on the treated area and occasionally small intumescences occurred. Methylcholanthrene and benzpyrene (1.5 per cent in lanolin) which are known to be very active carcinogenic agents for animals, produced necrosis of the treated decapitated internode without interfering with axillary bud development (fig. 12). Roots were sparsely produced on these young plants on the internodes below the treated area. Axillary buds below the treated area also developed in these treated plants, as shown in figure 13. The two young plants of same age and size shown in figure 14, grown under similar conditions, one of which was treated with methylcholanthrene and the other with indoleacetic acid, produced morphologically similar nodular masses on the treated internode and the methylcholanthrene specimens also produced roots.

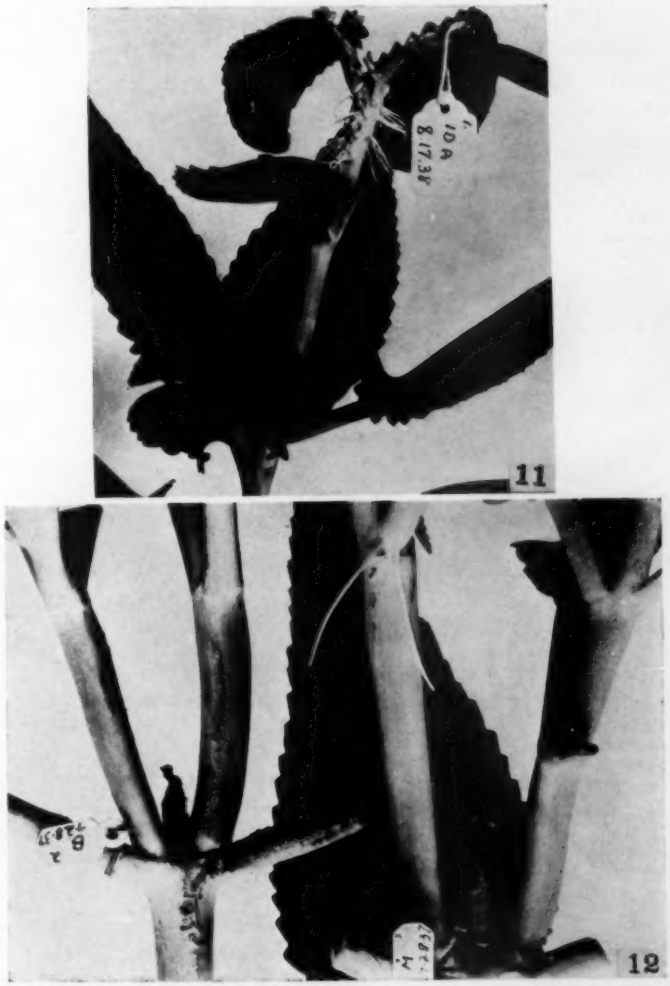


Fig. 11. Another plant of the same species 12 days after treatment with 3% indoleacetic acid in lanolin. ×¾.

Fig. 12. Kalanchoë stems treated with carcinogenic hydrocarbons showing necrosis of treated parts, photographed two and a half months after treatment. ×¾.

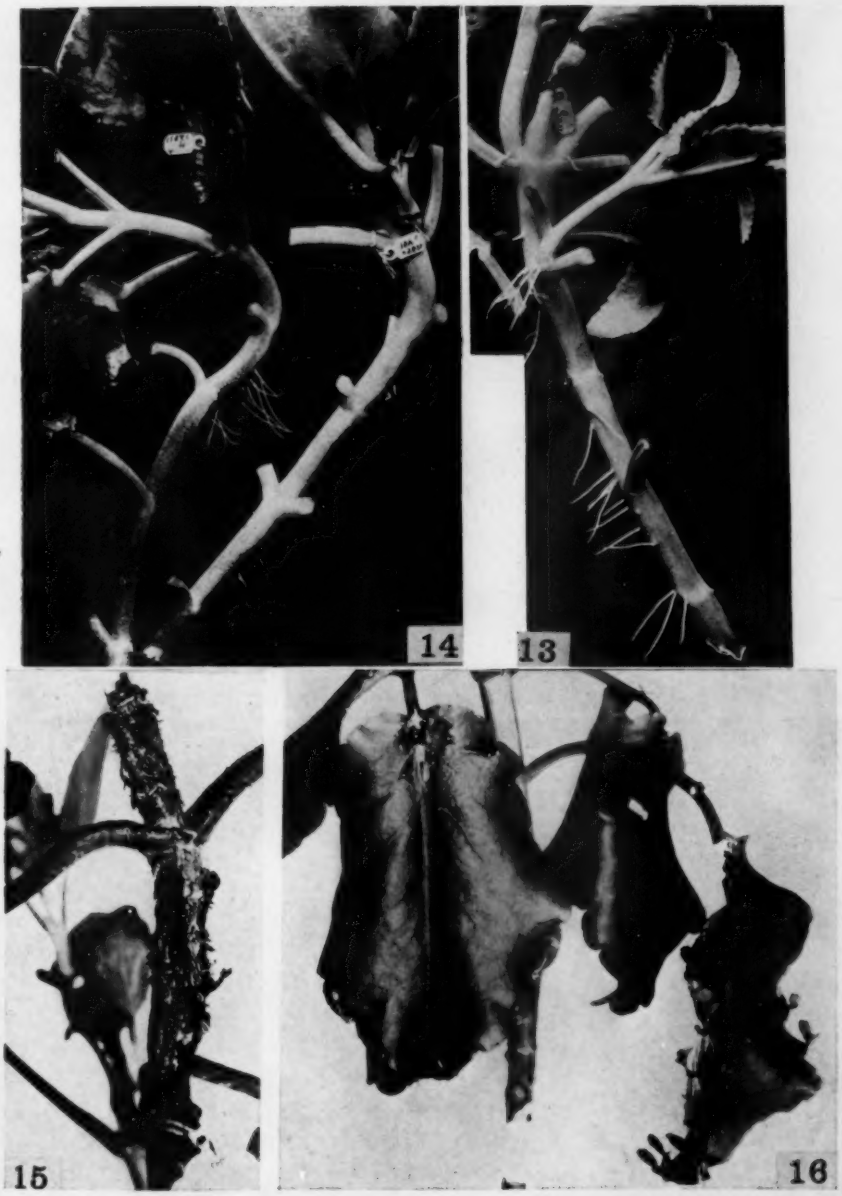
Stems of *Nicotiana glauca* when injured and treated with 1, 2, 5, 6-dibenzanthracene, benzpyrene, or methylcholanthrene in lanolin and applied with a glass rod over the injured area, do not produce roots. Three months after treatment swellings and ridged surfaces are produced. Microscopic studies of these tissues show aberrant, histological structures, which show considerable hyperplasia. The sections show distortion of the fibrovascular bundles due to extra cambial proliferation, with differentia-

tion into cortical and pith cells. The pictures are those of bizarre structures with hypertrophies and hyperplasias, and yet there are characteristics which make these reaction tissues no other than responses to injury. Stems of the tomato plant treated similarly with these carcinogenic agents produce unresponsive injuries or simple calluses.

BRYOPHYLLUM

Bryophyllum calycinum Salisbury, a species closely related to the Kalanchoë behaves unlike it in its responses to the agents used. A decapitated and injured stem of a young *Bryophyllum* (fig. 15) covered with a 3 per cent suspension of indoleacetic acid in lanolin a month previously, shows a reaction much like those observed in the sunflower. The stem cracks and numerous small root-like structures cover the surface of the treated internode. Small nodular masses occur which shrivel shortly after they are formed. The roots here are short, twisted and are not like the structures on Kalanchoë after treatment. The roots degenerate and the reaction process ceases. When the basal portion of the blade of young leaves were injured and treated with heteroauxin, plantules with comparatively long roots were formed as shown in figure 16. These leaves were young when they were treated and the photograph was made a month afterward. No nodules at the leaf base were observed in response to this treatment. Control *Bryophyllum* leaves, treated with lanolin, show no other response than scarring.

Methylcholanthrene or benzpyrene applied to decapitated and injured stems of *Bryophyllum* produce necrotic effects. The axillary bud development was not impaired. The indoleacetic acid applied to an injured portion of the stem induced small roots and slight protuberances over the treated zone as shown in figure 17. No roots were formed above or below the treated areas on these stems as on *Kalanchoë*. Sections of the indoleacetic acid treated *Bryophyllum* stems shown in figure 17 were studied. In figure 18 such a section is shown with a strand of fibrovascular bundles surrounded by parenchymatous cells, the outer layer of which appears to be atypical. Under higher magnification (fig. 19) comparatively large cortical-like cells are seen surrounding a number of irregular scalariform xylem vessels. The cells are part of a new growth which appears to have reached its maximum development. As in the *Kalanchoë*, the heteroauxin is capable of inducing slight hyperplastic tissue which matures rapidly, and appears to function only as a protective mechanism. These observations on the *Kalanchoë* and *Bryophyllum* seem to indicate that possibly too large a concentration of the carcinogenic agents was used. Yet, smaller doses have so far shown no different effect. The formation of roots and the development of the axillary buds indicate a specific host



Figs. 13–14. Kalanchoë stems treated with indoleacetic acid, methylcholanthrene, and 3, 4-benzpyrine. Note root formation, two and a half months after treatment. ×¾.

Fig. 15. *Bryophyllum calycinum* decapitated and treated with 3% indoleactic acid. Note cracked stem, short roots. ×¾.

Fig. 16. Leaves of *B. calycinum* with basal portion treated after injury with 3% indoleacetic acid. ×¾.

reaction independent of the agent used. *Kalanchoë* when stimulated, even only by amputation of the apical growing point, will liberate a root forming substance—possibly a root forming hormone. Under conditions still unknown, the application of scharlach red and possibly indoleacetic acid cause groups of sensitive cells to proliferate forming small overgrowths which resemble histologically crown gall tissue. The general experience with the growth substances in this laboratory, shows that so-called chemi-

Fig. 17. Bryophyllum stems two and a half months after treatment with indoleacetic acid, methylcholanthrene, or benzpyrene. ×¾.

Fig. 18. Section through the reaction tissue induced by indoleacetic acid on Bryophyllum stem shown in figure 17. ×30.

Fig. 19. Portion of section shown in figure 18 under higher magnification. ×200.

cal tumors are small, short-lived, and lack the proliferating power which cells have when stimulated by the organism *B. tumefaciens*. From an oncological point of view, tumor cells possess the power of limitless proliferation. When such groups of cells invade and destroy surrounding tissue, metastasize to other parts of the animal body, such tumors constitute malignant cancer. It appears from the present observations that these indoleacetic acid reactions do not fall in the category of crown gall or animal cancer. Response of cells to heteroauxin indicate a group of reactions more active than callus formation resulting from injury; a somewhat progressive, protective mechanism which is soon exhausted. Histologically, these small growths bear resemblance under certain conditions to crown gall tissue. It has been contended that crown gall, too, is a protective mechanism, the tissues of which proliferate because of the presence of bacteria.

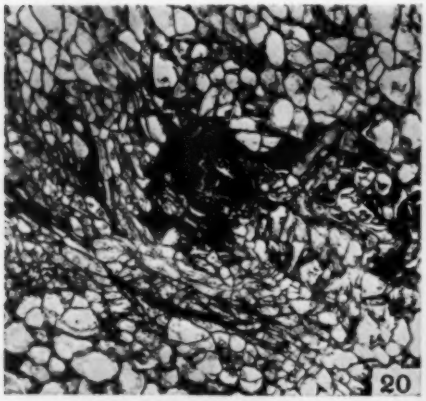
PHASEOLUS VULGARIS

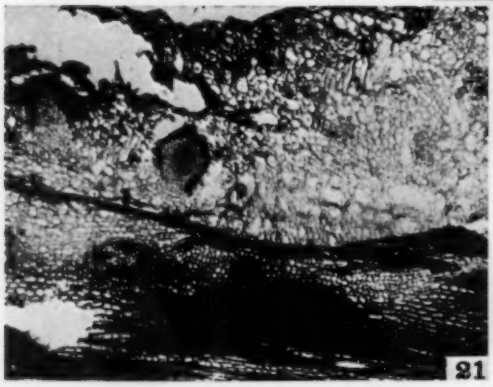
The effects of indoleacetic acid in lanolin on *Phaseolus vulgaris*, red kidney bean, have been studied intensively by Hamner and Kraus (1937). In this laboratory similar studies have been made for a number of seasons in the open garden. Young plants decapitated by removing the growing point, injured with a sterile needle, and covered with the agent, show a number of small nodular masses which form a somewhat globular structure on the treated area. On microscopic examination one notes rapid proliferation and differentiation of the various tissues. Root anlagen are frequently found imbedded in the tissue. These growths are characterized by the rapidity with which they arise and the rapidity with which growth ceases. *Cleome* sp., the common spiderwart, two to three feet tall, when decapitated and treated with indoleacetic acid, present reactions similar to those on the bean.

Young pods of the kidney bean, when injured and treated with indoleacetic acid, produce an overgrowth in which roots have not been observed. The new growth consists of rapidly proliferating tissue in which binucleate and uninucleate cells are found. Figure 20 shows a section of the reaction tissue from a pod, 14 days after treatment with heteroauxin. In this preparation internal necrosis of the tissue has already started. The tissue dries leaving a small shriveled, tough, fibrous mass. The viable cells still show clearly well-differentiated nuclei. The induced overgrowth on these pods is short-lived and its proliferating capacity is limited. This may be associated with the natural tendency of the pod to dry with the maturity of seeds. These treated pods produce few or no seeds.

Stems of the kidney bean injured and treated with indoleacetic acid occasionally show extensive proliferation. Here, as in the pod studies,

there is an active proliferation of cells over the treated zone. The cortex and cambium appear to be stimulated; there is anisocytosis with a preponderance of hypertrophied cells. Figure 21 shows a portion of a longitudinal section of such a stem. The cortical tissue shows growth activity.





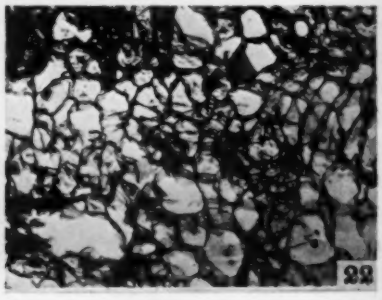


Fig. 20. Section from an overgrowth on the pod of the *Phaseolus vulgaris* treated with 3% indoleacetic acid in lanolin 14 days previously. ×200.

Fig. 21. Portion of stem of *P. vulgaris* treated as above. Note thick woody tissue and hyperplasia of cortex with root anlagen. ×30.

Fig. 22. Portion of figure 21 under higher magnification. ×200.

Fig. 23. A portion of a decapitated stem of *P. vulgaris* showing well organized roots; treated with indoleacetic acid 14 days previously. ×30.

Rudimentary roots are seen imbedded in the stimulated cortex. Breaking down of the tissue occurs within a period of two weeks after the treatment is made. Figure 22 shows a portion of figure 21 under higher magnification. The peripheral cortical cells are shrunken and take the safranin stain deeply. The more centrally placed cells show one or two nuclei. There is

evidence that there has been proliferative activity. Cell divisions have not been found at this stage.

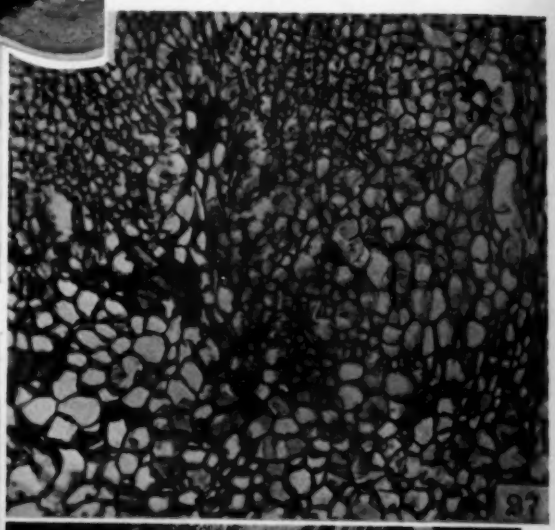
Under more favorable conditions when treatments are made nearer the growing point, cortical proliferations abound with differentiation of tissue into well-organized root-like structures, as shown in figure 23. The predominating cells are of the cortical type, two nuclei appear in the larger cells. Here the evidence of a neoplastic disease of the crown gall type is not present.

It appears that in the reaction tissue of the kidney bean, induced by injury and application of indoleacetic acid in lanolin, there is present an increased response over that induced by injury alone. There is unquestionably a stimulus to proliferation which appears to be induced by heteroauxin. Yet these stimulated cells appears to be incapable of transmitting to the daughter cells, even to the limited extent shown by some crown gall tissue, the power to multiply. These cells stimulated, divide apparently for several generations; they differentiate and grow old, and in the absence of means for maintaining their nutrition, they die. The relationship between these reaction tissues and their effects on the host is not clear. In many instances the death of the reaction tissue occurs with the death of the stem upon which they arise. In other instances the death of the reaction tissue has no effect upon the host. The possible factor that determines the death of the treated part of the host tissue is the degree and intensity of injury which ultimately interferes with nutrition. There is no indication available to show that the new growth invades or spreads in the host tissue.

HELIANTHUS AND BRASSICA

Heteroauxin, Auxin, Vitamin B_1 and Nicotinic Acid.—The possibility of stimulating heteroauxin treated cells to greater proliferating power has been investigated. The results obtained with a limited number of agents are significant and may be mentioned at this time. It is now well known that the production of tar cancer in animals involves repeated applications of the agent. The carcinogenic hydrocarbons, however, may induce malignant neoplasia through a single injection. The studies reported previously (Levine, 1934) have shown that a single application of scharlach red or tar on *Helianthus* or *Ricinus*, appears to be as effective as repeated paintings. The newly formed cells, it seems, are incapable of further response after the first painting with the agent. Overgrowths comparable with crown gall were not produced.

The immature inflorescences of broccoli, young leaves of the oat, apical shoots of hollyhocks, were extracted with acidulated chloroform. The residue, after drying *in vacuo*, was weighed and 150 mg. to 200 mg. of



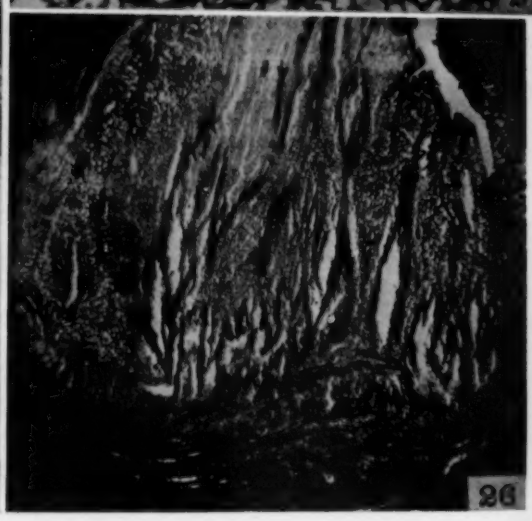


Fig. 24. Sunflower stems treated with 3% indoleacetic acid three times at intervals of 12 days and eight days—fixed two weeks after the third treatment. ×¾.
Fig. 25. Section of the stem through the treated area shown in figure 24. ×7½.
Fig. 26. Portion of figure 25 showing organoids. ×30.
Fig. 27. Basal portion of a structure shown in figure 26. ×200.

each was mixed with 5 gm. of lanolin. These agents were applied at varying intervals to stems of sunflowers, castor bean, and tomato plants treated

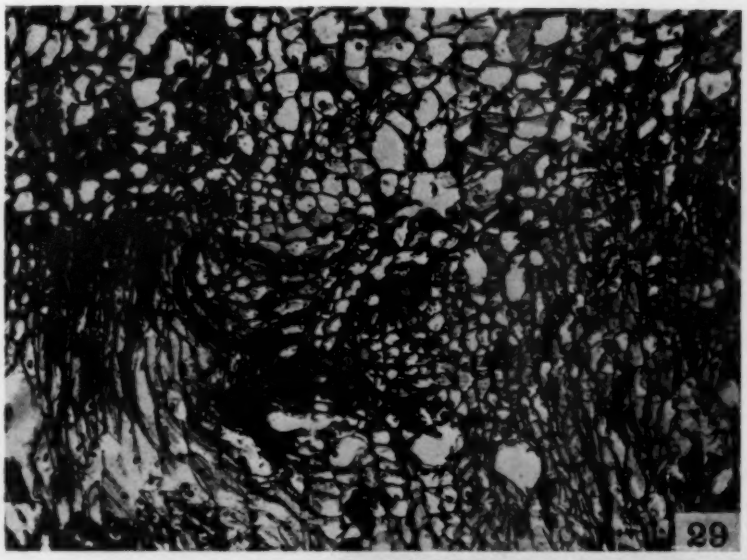


Fig. 28. Stems of sunflower treated with 3% indoleacetic acid followed by two application of vitamin B_1 in lanolin, 12 days and 8 days apart. Fixed two weeks after last treatment. $\times 3/4$.

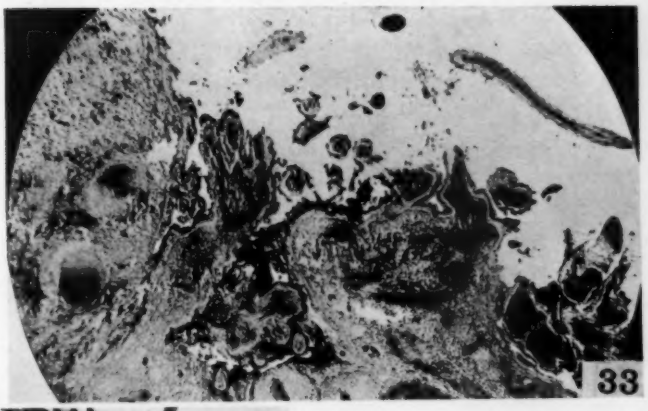
Fig. 29. Section from the stem on left shown in figure 28. $\times 200$.

Fig. 30. Sunflower stem treated with lanolin after apical injury fixed 53 days after treament. $\times 30$.

with 3 per cent indoleacetic or scharlach red in ether. In subsequent studies crystalline vitamin B_1, and nicotinic acid hydrochloride were rubbed up with lanolin to make a 1.2 per cent to 1.8 per cent suspension. These were used on plants after lanolin indoleacetic acid applications had been made after injury. The auxin and the nicotinic acid suspension proved ineffective and were discontinued. Figure 24 shows two sunflower stems treated with 3 per cent indoleacetic acid in lanolin. This was followed, 13 days later, by a like treatment with indoleacetic acid. A week later a similar application was made. At the time the second application of heteroauxin was made, there appeared to be a cessation of growth activity of the treated area. Following the second application, new organoids or club-shaped structures appeared. Many of these resembled root-like structures. This activity became quiescent and after applying the heteroauxin for the third time, there again appeared new organoids. The photograph was taken 36 days after the first treatment. The overgrowths are raised above the surface of the stem.

A portion of a cross section of one of the stems through the treated area is shown in figures 25 and 26. The pith shows evidence of growth disturbances induced by cell proliferation. The wood is increased in thickness and the cortex has been invaded by strands of fibrovascular elements. Club-shaped bodies consisting of parenchymatous tissue together with strands of definitely oriented fibrovascular elements seem to have arisen from the outer surface of the fibrovascular bundles. These structures branch and resemble the calloid structures on tobacco hybrids (Levine, 1937). Examination of the tissue at the base of the organoids, reveals small cells of embryonic type (fig. 27) arising from much larger parenchymatous cells.

Brassica oleracea botrytis treated on two occasions over the same area with indoleacetic acid in lanolin show interesting results comparable with those mentioned above. Figure 31 shows two stems of Italian broccoli, one of which was decapitated and pricked with a sterile needle on the cut surface and then covered with heteroauxin-lanolin paste. This treatment was repeated three weeks later and the tissue was fixed two weeks afterward. The other plant was injured similarly at the base of the stem and treated only once with the same paste and fixed two and one-half months after treatment. The amputated stem shows numerous nodular bodies which consolidated into a flattened globular mass. Microscopically, this mass consists of parenchymatous bodies in which few vascular elements are seen (fig. 32). The reaction at the basally treated plant shown in figure 31 consists of comparatively long, dried roots with small knob-shaped protuberances. On sectioning this tissue, many disoriented organoids were found as shown in figure 33. Some were long, stem-like struc-



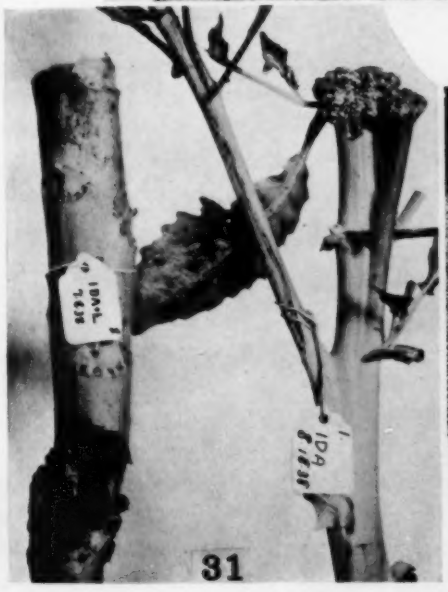


Fig. 31. Stems of broccoli decapitated and treated twice with 3% indoleacetic acid three weeks apart. Stem to the left treated at base once with paste of indoleacetic acid in lanolin, after being injured. ×¾.

Fig. 32. Section of decapitated broccoli shown in figure 31, 14 days after last treatment. ×30.

Fig. 33. Section of basally treated broccoli shown in figure 31. ×30.

tures, others consisted of short, thickened structures composed of parenchymatous cells similar to those shown in figure 32. The double treatment of the decapitated stem seems to have affected the size of these reactions. This increased size, however, was due to the stimulation of the host tissue. Cells once stimulated appear to be little influenced by repeated treatments.

Figure 28 represents two sunflower stems injured and treated with 3 per cent indoleacetic acid and followed by an application of vitamin B_1 in lanolin two weeks later. Another treatment with the vitamin was made two weeks after the second treatment. The tissue was fixed 36 days after treatments began. Here as in the repeated indoleacetic acid treated stems, there were no added stimulations to the reaction tissues. New structures seemed to arise. Figure 29 is a section of the stem shown in figure 28. The tissue consists of cortical cells in which protoxylem-like cells are present. These elongated members are possibly the precursors of fibrovascular elements. This tissue presents no unusual appearance other than that of a callus. There is apparently no marked difference between the multiple indoleacetic acid treated plants and those subjected to heteroauxin followed by application of vitamin B_1.

Sunflowers used as controls were treated with hydrous lanolin after injury. Figure 30 shows a section through the area of treatment of such a stem made 53 days after the application of lanolin. There is callus formation with limited new growth. New or distorted fibrovascular bundles are seen with proliferations of the wood and cortex. Lanolin has a distinct protective value and the injured tissue appears to be able to respond better under the influence of a covering of lanolin than without it.

SALIX FRAGILIS

The contention that the action of *Bacterium tumefaciens* on plants grown in a solution containing tryptophane is similar to the action produced by indoleacetic acid is held by Brown and Gardner (1936), Berthelot and Amoureux (1938), Link (1937[2]) (1938). The differences in the response resulting from inoculation of *B. tumefaciens* and the reactions induced by the application of indoleacetic acid appear to be overlooked. Riker (1939) has called attention to the similarities in reactions due to inoculation with *B. tumefaciens* and treatment with indoleacetic acid.

The following experiment used to test the root producing ability of an organism or chemical is of interest, and seems applicable here. Willow branches (*Salix fragilis*) removed from the tree either in winter or summer, when stripped of leaves, cut into convenient sizes, and placed under bell jars over water, produce shoots from the apical end of the stick and roots at the basal end. The application of indoleacetic acid to the apical end of the stick as shown by Fischnich (1938) for *Populus nigra* var. *pyramidalis* and repeated here on *Salix fragilis*, shows the formation of roots along the length of the cutting, with complete suppression of shoots. Other synthetic growth substances give similar results. The application of a virulent culture of *B. tumefaciens* grown in bean agar, to the apical cut surface of these willow sticks results in shoot formation from the apical

Fig. 34. Sticks of *Salix fragilis* treated apically: ×¾.

1st—Cut surface covered with active culture of *B. tumefaciens.*
2nd—Both upper surfaces of split stem covered with lanolin—apical shoots.
3rd—Left half split stem covered with lanolin-apical shoots; right half covered with lanolin paste with indoleacetic acid—apical roots.
4th—Lanolin control.
5th—Woolly knot organism.
6th—*Phytomonas rhizogenes.*

leaf scars and roots at the basal end. *P. rhizogenes*, the woolly knot organism, and lanolin controls showed similar results (fig. 34). There is apparently no interference with the normal tendency of the sticks to produce shoots apically and roots basally. The application of a mixture of a culture of *B. tumefaciens* (400 mg.) and tryptophane (9 mg.) to the apical cut surfaces of a number of willow sticks, suspended in a moist chamber produced only roots with abundant lenticular proliferations. In five to seven days the sticks show responses similar to that induced by the application of indoleacetic acid in lanolin alone. The application of a mixture of bean agar or an equal quantity of lanolin with tryptophane (3 per cent) was next applied to willow sticks and placed in moist chambers. Five to seven days later, the sticks produced normal leaf shoots at the apical end and roots at the basal end. *B. tumefaciens* apparently acted on the tryptophane forming a root stimulating substance like indoleacetic acid. It appears from this test that *B. tumefaciens* grown in white bean agar does not effect the normal course of shoot development in the willow cuttings. The reaction of the crown gall organism grown in tryptophane may be that of a root stimulating substance, indoleacetic acid.

Roots appear on crown galls on plants which have a tendency to form roots. Tobacco, *Nicotiana tabacum*, produces crown galls with numerous leafy shoots, while *Kalanchoë* and *Bryophyllum* stems produce crown galls with both roots and shoots.

It would appear that the host rather than the inciting organism determines the nature of the response. There is no evidence adduced to show that the mechanism in crown gall formation is due to the presence of indoleacetic acid. Here and in material previously presented, it has been shown that the response of plants to application of indoleacetic acid is primarily one of root formation in susceptible hosts. Limited hyperplasia and hypertrophy occur in the tissue response but these cells are not endowed with proliferating power sufficient to produce overgrowths comparable with crown gall. Under certain conditions, in the *Kalanchoë*, the application of scharlach red has induced crown gall-like structures. In this same species and others reported above, indoleacetic acid produces tissue responses which present histologically the tissue characteristics of crown gall. The gross morphological manifestations do not appear to be comparable.

The suggestion that these responses on plants induced by chemical agents and injury are tumors, cannot be accepted unless the plant tumor concept is different from that imposed by the animal pathologist. However, some of these reactions appear to be more than simple callus formations. They are composed of hypertrophied and hyperplastic cells forming an aberrant organization yet with limited power of proliferation. From these

facts it is conceivable that these chemical responses may be placed in the category of neoplastic diseases in a grade lower than crown gall.

SUMMARY AND CONCLUSIONS

The data presented deal with the attempt to produce cancerous growths on plants by means of carcinogenic agents or growth substances. This report covers the results of experiments for a period of two years during which many species of plants were used, principally, *Kalanchoë*, *Bryophyllum*, sunflower, kidney bean, tobacco, and broccoli. These plants were treated with certain carcinogenic hydrocarbons or other substances such as scharlach red, heteroauxin, auxins, and vitamin B_1. Repeated treatments of indoleacetic acid, and indoleacetic acid followed by treatment with vitamin B_1 were also employed.

Scharlach red which has been reported carcinogenic for certain laboratory animals has been found active in some cases with *Kalanchoë Daigremontiana*. The application of 1 per cent of this dye in ether to the apical internode after decapitation produces overgrowths which resemble crown galls. Other carcinogenes like 1, 2, 5, 6-dibenzanthracene, 3, 4-benzpyrene, methylcholanthrene induce necrosis of the treated zone. Roots, subsequently, appear in the internodal spaces below the treated areas in *K. Daigremontiana*. *Bryophyllum calycinum* treated, similarly, failed to produce roots.

The effects of indoleacetic acid in lanolin on decapitated and injured stems induces root formation. The stems crack, and small nodular masses are formed. Small overgrowths on decapitated kalanchoës present histological pictures which are identical with crown gall. In the most abundant overgrowth found so far, described by Hamner and Kraus (1937) and reported here, the heteroauxin treated pods of kidney bean present microscopical pictures very much like that found in the crown gall, but the life of the new growths are comparatively short.

Repeated treatment of stems of sunflower or broccoli with indoleacetic acid or indoleacetic acid followed by vitamin B_1, produces raised overgrowths which consist of calloid structures made up of parenchymatous tissue as well as root-like structures. These treatments fail to produce excessive overgrowth.

The fundamental difference between the heteroauxin induced overgrowth and crown gall is the limited proliferation power of the former. The chemically stimulated cells perpetuate themselves for only a few cell generations. In the most active indoleacetic acid overgrowths, cell proliferation is limited, differentiation rapid, and life of the tissue comparatively short. *Bacterium tumefaciens* under favorable conditions, induces a variety of discrete overgrowths, of which the globular type is most common.

Leafy crown galls and crown galls with roots represent other forms. The gall itself consists of parenchymatous tissue of the embryonic cell type. Longevity of this tissue is comparatively great and differentiation occurs over a long period, ultimately causing woody and corky tissue, and death. No experimental evidence has been adduced to show that the crown gall cell can proliferate in the absence of *B. tumefaciens*. Histologically, crown gall and some of the chemically stimulated overgrowths appear to be alike. Their gross morphological structures are widely different.

Reaction of plants to the crown gall organism and chemical agents are protective mechanisms comparable only to inflammation in animals and man. The proliferating power of the cancer cells is limitless. This results in invasion of normal tissue and metastatic secondary tumors. Transplantation of cancer tissue is possible for many transplant generations. The ability of these chemically induced reactions to transplant has not been attempted. Crown gall tissue has limited transplantability as contended by Jensen. The graft mechanism is complicated by the presence of *B. tumefaciens* in the inoculum.

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Additions to Florida Fungi—IV

WILLIAM A. MURRILL

Work on plant diseases in Florida is still only preliminary, in spite of all the excellent things that have been accomplished; and this is particularly true of diseases caused by the basidiomycetes. Many of the species in this large group are still unknown and the harm they do still unsuspected. A good illustration of this may be found in *Corticium, Thelephora, Hydnum, Merulius,* or *Poria.*

Among the larger polypores, which have probably received most attention, *Fomes marmoratus* and *F. supinus* are exceedingly abundant on hardwoods; *F. Curtisii* and *F. lucidus* on oak, maple, ash, etc.; *F. Calkinsii* is frequent on live-oak; *F. annosus* on pine; and *F. tornatus* on a variety of trees. *Fomes geotropus* still presents a problem, occurring as it does on several hardwoods and also on cypress. *Polyporus hispidus* is all too common on oaks, and *P. ludovicianus* is fully as threatening, appearing frequently on shade trees along city streets. *P. sulphureus* is another common and destructive tree parasite, which even occurs in South America. *P. fissilis* attacks the trunks of species of oak, *P. persicinus* the roots of the live-oak, and *P. Schweinitzii* the roots of various pines.

Idle and meaningless words, most of them; for what do we really know about the life history and effects of these fungi on the trees in Florida? Pathologists have always been glad to accept assignments to this state during the winter, when most things are dormant, but they rush to get out before real activity begins. There is still a vast opportunity for the patient investigator here, where the forest will always be a dominant factor.

When we turn to the gill-fungi, *Clitocybe tabescens* looms big. There is scarcely a tree or shrub which it will not attack. I have seen magnificent shade trees wilt and die without apparent cause until tell-tale mushrooms sprang up about their base. *Armillaria mellea* is also active but the sporophores are rarely seen. Sometimes a large crop will come out in midwinter. *Lentinus lepideus,* like other members of its large group, thrives under subtropical conditions. I have seen it all the way to Buenos Aires. *Schizophyllus alneus* is one of the fastest-working agarics I know. It has to be to fruit on a rotten apple. *Pleurotus ostreatus* is very abundant in Florida, as are species of *Flammula* and the bitter clusters of *Hypholoma fasciculare* springing up from the roots of trees.

Enough has probably been said to suggest the importance of more work on the Florida fungi. During the past few years I have been attacking the problem in a taxonomic way, devoting particular attention to Alachua County, situated near the center of the state in a region rich in both pine-

lands and hammocks. The numbers cited in the following discussion of new species from this region represent collections in the Herbarium of the Florida Agricultural Experiment Station, at Gainesville, where Mr. Erdman West is mycologist, and all my work has received his enthusiastic support.

Coltricia Mowryana sp. nov.

Pileo flabelliformi, 7–10 cm. lato, multizonato, fulvo, lobato; tubulis castaneis, angulatis, 5–8 mm. longis; sporis fulvis, 8–9 × 4–5μ; stipite eccentrico, fulvo, tomentoso, 2–4 × 1 cm.

Pileus flabelliform, plane to slightly depressed, gregarious, 5–8 × 7–10 × 0.5–1 cm.; surface radiate-sulcate, multizonate, innate-radiate-fibrillose, shining, fulvous; margin lobed, isabelline in younger stages, sterile for about 2 mm.; context very thin, fibrous, tough, fulvous; hymenium slightly determinate-decurrent, even to somewhat rough and pitted with age, castaneous to fuliginous in mature specimens, ferruginous on the sterile marginal band; tubes entire, angular, thin-walled, 5–8 mm. long, 3 to a mm.; spores ellipsoid or ovoid, smooth, fulvous, granular, 8–9 × 4–5μ; cystidia none; stipe eccentric, equal, cylindric, densely velvety-tomentose, fulvous, 2–4 × 1 cm.

Type collected by W. A. Murrill in the decayed hollow trunk of a living red bay, *Persea borbonia* Spreng., in Sugarfoot Hammock, near Gainesville, Fla., Nov. 7, 1938 (*F 18391*). Also collected by the author on a rotten log of red bay in South Planera Hammock, eleven miles northwest of Gainesville, Oct. 30, 1938 (*F 18375*). Rarely seen and probably confined to this one host. Practically all the trees of this species in the vicinity of Gainesville are hollow and partly decayed. This polypore may be the active agent. Another species often found here in the hollow trunks of red bay is *Hapalopilus licnoides* (Mont.) Murrill, but it grows abundantly on various kinds of dead wood. Mr. Harold Mowry, to whom this interesting new species is dedicated, is Director of Research in the Florida Agricultural Experiment Station.

Gymnopilus subdryophilus sp. nov.

Pileo convexo-subexpanso, 5–6 cm. lato, fulvo, praefelleo; lamellis sinuatis, latis, sporis 5–6 × 3–4μ; stipite flavido, 4–6 × 0.3–1 cm.

Pileus convex to subexpanded, gregarious to cespitose, 5–6 cm. broad; surface becoming smooth and glabrous, fulvous, margin even, entire; context very bitter at once; lamellae sinuate-decurrent, broad, rather crowded, inserted, entire, ochroleucous to ferruginous, at length fulvous; spores ellipsoid, smooth, ferruginous, 5–6 × 3–4μ; stipe tapering upward, smooth, glabrous, whitish-

mycelioid at the base, pale-yellowish, 4–6 × 0.3–0.5 cm., reaching 1 cm. at times at the base.

Type collected by W. A. Murrill on an oak log near Magnesia Springs, Fla., May 27, 1938 (*F 16226*). Also collected by E. West on an oak log at Newnan's Lake, July 7, 1938 (*F 17486*). Not rare on oak logs about Gainesville. It is not scaly like *G. dryophilus* Murrill and the taste is exceedingly bitter instead of mild. From *G. amarissimus* Murrill it differs in growing on hardwood and having much smaller spores.

Galerula alachuana sp. nov.

Pileo conico-convexo, 5–7 mm. lato, striato, avellaneo-isabellino; lamellis adnatis, sporis 12–14 × 7–8μ; stipite stramineo, 6 × 0.1 cm.

Pileus conic to convex, gregarious, 5–7 mm. broad; surface dry, glabrous, striate, avellaneous-isabelline, isabelline on the small umbo, margin straight, entire; lamellae adnate, ventricose, broad, inserted, medium distant, entire, fulvous, with white edges; spores ellipsoid, smooth, granular, deep-ferruginous, 12–14 × 7–8μ; cystidia none; stipe tapering upward, smooth, glabrous, stramineous, about 6 cm. long and 1 mm. or less thick.

Type collected by West, Arnold and Murrill in moist soil under hardwood trees at Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 21, 1938 (*F 18326*). Also collected by the same persons on the ground in Sugarfoot Hammock, Oct. 18, 1938 (*F 18318*). Suggesting *G. tenera* (Schaeff.) Murrill and having similar spores but differing in several ways. It never occurs on lawns but only in low, wet hammocks.

Naucoria appendiculata sp. nov.

Pileo late convexo, 1.3 cm. lato, isabellino, striato; lamellae adnexis, albofimbriatis, sporis ellipsoideis, 6 × 3–4μ; stipite pallido isabellinoque, 4 × 0.1 cm.

Pileus broadly convex, solitary, 1.3 cm. broad; surface dry, glabrous, isabelline, subfulvous on the disk, margin entire, striate, appendiculate; context membranous; lamellae adnexed, rounded behind, broad, medium distant, inserted, fulvous, the edges white-fimbriate; spores ellipsoid, smooth, pale-ferruginous under the microscope, 1-guttulate, about 6 × 3–4μ; cystidia none; stipe equal, smooth, finely fibrillose and pallid above, squamulose and concolorous below, 4 × 0.1 cm.

Type collected by West, Arnold and Murrill on an oak log in Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 21, 1938 (*F 18367*). The spores are doubtless fulvous in mass, the color of the mature gills. The small veil does not leave a ring.

Hebeloma floridanum sp. nov.

Pileo convexo-expanso, umbonato, 3.5 cm. lato, viscido, stramineo; sporis ovoideis, 8 × 5μ, cystidiis 40 × 15μ, stipite albo, 5 × 0.5–0.6 cm.

Pileus convex to expanded, umbonate, gregarious, 3.5 cm. broad; surface viscid, smooth, shining, glabrous, stramineous, margin even, entire; context white, unchanging, without characteristic odor or taste; lamellae adnexed with decurrent tooth, ventricose, medium broad and medium distant, inserted, pallid to discolored, edges fimbriate; spores ovoid, smooth, ferruginous, 1–guttulate, about 8 × 5μ; cystidia bottle-shaped, hyaline, blunt and crested at the tip, projecting about 40 × 15μ; stipe equal, smooth, shining, glabrous, white, furfuraceous at the apex, 5 × 0.5–0.6 cm.

Type collected by W. A. Murrill under hardwoods in a high hammock at Gainesville, Fla., Oct. 17, 1938 (*F 18365*). Having the usual appearance of *Hebeloma* with cystidia like those of *Inocybe* and spores resembling those of *Cortinarius*. They are umbrinous in mass and ferruginous under the microscope.

Crepidotus praelatifolius sp. nov.

Pileo dimidiato, gregario, 1–2 mm. lato, albo, piloso; lamellis praelatis, sporis globosis, 6μ.

Pileus fleshy, sessile and dimidiate or conchate to resupinate, densely gregarious, imbricate, often laterally confluent, 1–2 mm. broad; surface white, unchanging, covered with long, white, delicate hairs, margin even, entire; context white, membranous, becoming inconspicuous at maturity; lamellae very few, very broad, entire, pallid to fulvous, becoming folded and irregular with age; spores globose, smooth, yellowish-brown, about 6μ.

Type collected by A. S. Rhoads on the bark of a dead magnolia log in Gainesville, Fla., Sept. 8, 1938 (*F 18107*). A very peculiar species, apparently related to *C. latifolius* Peck and *C. parvulus* Murrill. The tiny caps are little more than tufts of hairs holding the few large gills in position until the spores mature. Later, the gills become more prominent and little else can be seen on the substratum.

Entoloma subalbidum sp. nov.

Pileo convexo-subplano, 3–6 cm. lato, avellaneo vel albo, farinaceo; lamellis confertis, sporis angulatis, 8–10μ; stipite albo, glabro, 5–7 × 0.6–0.8 cm.

Pileus convex to nearly plane, gregarious, 3–6 cm. broad; surface smooth, glabrous, opaque and pale-avellaneous when fresh and moist, white and shining when losing the moisture, avellaneous in the herbarium; margin incurved, even and entire, rimose at times with age; context whitish, opaque, with strongly

farinaceous odor and taste; lamellae sinuate, narrow, crowded, inserted, broadest behind, uneven, toothed, white to pink; spores decidedly angular, apiculate, 1-guttulate, pink, 8–10μ; cystidia none; stipe equal or tapering upward, smooth, glabrous, white, shining, 5–7 $\times$ 0.6–0.8 cm.

Type collected by West and Murrill on the ground under hardwood trees in South Planera Hammock, about eleven miles northwest of Gainesville, Fla., Oct. 26, 1938 (*F 18311*). Suggesting *E. albidum* Murrill and also near *E. Grayanum* (Peck) Sacc. Found in abundance, some of the drier hymenophores being milk-white and shining, while others were hygrophanous on the margin and still others opaque and avellaneous over the entire surface. After a few hours, however, in the electric oven, they all took on the same avellaneous shade.

Russula clitocybiformis sp. nov.

Pileo convexo-praedepresso, 4.5 cm. lato, albido, subtomentoso, sapore grato; sporis globosis, albis, 9–11μ, stipite albo, 3 $\times$ 0.8 cm.

Pileus convex to deeply depressed, solitary, 4.5 cm. broad; surface slightly viscid, finely tomentose, dirty-white, margin even, entire, strongly deflexed on drying; context very thin, white, unchanging, odorless, mild or nearly so; lamellae adnate, some forking at the base, narrow, rather close, inserted, entire, thin, white, unchanging; spores globose, spinulose, white, 9–11μ; sterile cells abundant, spinulose, sharp, smooth, hyaline, about 60–75 $\times$ 5–10μ; stipe equal, smooth, glabrous, white, unchanging, 3 $\times$ 0.8 cm.

Type collected by West, Arnold and Murrill under hardwood trees in Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 21, 1938 (*F 18366*). Having the appearance of a white *Lactaria* or *Clitocybe* when dried. A rare and interesting species.

Russula regalis sp. nov.

Pileo convexo-subdepresso, 9 cm. lato, vinoso, glabro, sapore grato; lamellis latis, adnatis, sporis ochraceis, echinulatis, 7–9μ longis; stipite albo, 3 $\times$ 1.5–2 cm.

Pileus convex to expanded, slightly depressed, solitary, 9 cm. broad; surface glabrous, polished, vinosous, slightly viscid, margin somewhat striate; context very thin, white, unchanging, odorless, mild; lamellae adnate, very broad, not depressed behind, a few forked behind and very few inserted, medium distant, fimbriate, becoming luteous at maturity; spores deep-yellow, subglobose to broadly ellipsoid, prominenty echinulate and somewhat reticulate, 7–9μ long; cystidia none; stipe slightly tapering downward, smooth, white, unchanging, glabrous, 3 $\times$ 1.5–2 cm.

Type collected by Dwight Lucas under oaks in Gainesville, Fla., Nov. 8, 1938 (*F 18371*). The luteous gills and purple cap make a royal color combination rarely displayed so vividly.

Russula rubrifolia sp. nov.

Pileo convexo-depresso, 9 cm. lato, atropurpureo, praefelleo; lamellis latissimis, adnatis, sporis globosis, albis, tuberculatis, 6–8μ; stipite roseo, 4.5 × 1.5–2 cm.

Pileus convex to deeply depressed, solitary, 9 cm. broad; surface somewhat viscid, pruinose to glabrous, atropurpureous or badious, margin even, undulate, not peeling at all; context thin, white, unchanging, odorless, very bitter at once; lamellae squarely adnate, some forked at the base, equal, ventricose, unusually broad, 1.5 cm. at least, entire, bright-red on the edges for their whole length; spores globose, white, 6–8μ, decorated with scattered warts, some of them elongate like a cock's comb; cystidia none; stipe tapering downward, smooth, glabrous, rose or incarnate, solid, white within, unchanging, 4.5 × 1.5–2 cm.

Type collected by W. A. Murrill on the ground in a forest of longleaf pines near Orange Heights, Alachua Co., Fla., Nov. 9, 1938 (*F 18387*). Suggesting large forms of *R. uncialis* Peck but with different habitat, color, taste, and gill characters. It is a beautiful and striking species, highly colored, with firm flesh, and drying without much change. Microscopic characters indicate a close relationship with *R. uncialis* and *R. purpurina*.

Lepiota phaeostictiformis sp. nov.

Pileo convexo-expanso, umbonato, 1.5–2 cm. lato, atro-squamuloso; sporis ellipsoideis, 5–6 × 3–4μ, stipite albo, pruinoso, 4–5 × 0.2–0.3 cm.; annulo albo et fusco.

Pileus convex to expanded, mammillate, gregarious to subcespitose, 1.5–2 cm. broad; surface dry, white with black scales, black on the broad disk, margin even, entire; context thin, white, unchanging, odorless; lamellae free, rounded behind, ventricose, rather broad and rather crowded, finely fringed, white, unchanging; spores ellipsoid, smooth, hyaline, 1-guttulate, obliquely apiculate, 5–6 × 3–4μ; stipe tapering upward from a somewhat clavate base, smooth, finely pruinose, white, unchanging, 4–5 × 0.2–0.3 cm.; annulus 1 cm. from the apex, fixed, persistent, double, the upper margin white and fimbriate, the lower membranous and fuscous.

Type collected by West, Arnold and Murrill on a rotten pine log in Prairie Creek Hammock, a few miles southeast of Gainesville, Fla., July 15, 1938 (*F 17839*). Also collected by W. A. Murrill on rotten pine wood in

a low hammock at Gainesville, Nov. 1, 1938 (*F 18325*). Closely related to *L. phaeosticta* Morgan, found on a log in Ohio.

Hydrocybe subminutula sp. nov.

Pileo convexo, 7–10 mm. lato, viscido, rubro; lamellis decurrentibus, latis, flavidis; sporis 5–6 × 3–4μ; stipite rubro, 1.5–2.5 × 0.1–0.2 cm.

Pileus convex to subexpanded, rarely depressed, gregarious, 7–10 mm. broad; surface viscid, smooth, glabrous, red, soon fading to yellow but often retaining the red color in the center, margin even, entire; lamellae arcuate, decurrent, distant, broad, inserted, entire, pale-yellow; spores ellipsoid, smooth, hyaline, granular, obliquely apiculate, 5–6 × 3–4μ; cystidia none; stipe viscid, smooth, glabrous, tapering downward, red, not soon fading, 1.5–2.5 × 0.1–0.2 cm.

Type collected by W. A. Murrill on low ground under hardwoods in Sugarfoot Hammock, near Gainesville, Fla., Nov. 7, 1938 (*F 18392*). The short stem and small spores separate it from near relatives. Found in abundance at one place. On drying the caps regain some of their lost color, becoming testaceous, while the stems remain red.

Clitocybe subeccentrica sp. nov.

Pileo convexo-umbilicato, 1.5–2.5 cm. lato, albo, glabro; lamellis confertis, sporis 6 × 4μ; stipite eccentrico, albo, 1.2–1.7 × 0.1–0.2 cm.

Pileus subcircular, convex to expanded, umbilicate, gregarious to cespitose, 1.5–2.5 cm. broad; surface dry, smooth, glabrous, uniformly white, unchanging, margin incurved, even, entire to undulate; context thin, white, odorless, fleshy, not reviving; lamellae decurrent, inserted, narrow, crowded, entire, yellowish or pale-rosy-isabelline; spores pip-shaped, smooth, hyaline, about 6 × 4μ; sterile cells few, subcylindric, smooth, hyaline, about 15 × 7μ; stipe equal, eccentric, smooth, subglabrous, white, whitish-mycelioid at the base, 1.2–1.7 × 0.1–0.2 cm.

Type collected by West, Arnold & Murrill on dead hardwood in Beech Woods, near Santa Fé, Fla., July 13, 1938 (*F 18385*). Suggesting *C. eccentrica* Peck but with different spores.

Prunulus subepipterygius sp. nov.

Pileo convexo-depresso, 1–2 cm. lato, viscido, sulcato; sporis ellipsoideis, 5–6 × 3–4μ; cystidiis subcylindricis, 15–30 × 15μ; stipite albo, glabro, 1–3 × 0.1–0.2 cm.

Pileus convex to plane, depressed at the center, gregarious to cespitose, 1–2 cm. broad; surface slimy-viscid, smooth, glabrous, sulcate, white, um-

brinous on the disk; context membranous, white; lamellae adnexed, narrow, tapering behind, medium distant, inserted, entire, white, unchanging; spores ellipsoid, smooth, hyaline, 1–guttulate, 5–6 × 3–4μ; cystidia subcylindric, smooth, hyaline, projecting 15–30 × 15μ, occupying the entire edge of the gill; stipe smooth, white, glabrous, viscid, ridged at the apex, 1–3 × 0.1–0.2 cm.

Type collected by West and Murrill on a hardwood log in Planera Hammock, eleven miles northwest of Gainesville, Fla., July 20, 1938 (*F 18363*). Also collected at the same place by West, Arnold and Murrill on an oak log, July 21, 1938 (*F 17910*). Evidently near *P. epiptery-gius* (Scop.) Murrill but having a shorter stem and smaller spores.

Prunulus syringescens sp. nov.

Pileo convexo, 1 cm. lato, subavellaneo; lamellis sinuatis, latis, sporis ovoideis, 5 × 3μ; stipite albo, glabro, 2.5 × 0.1 cm.

Pileus convex, not expanding, solitary, 1 cm. broad; surface dry, smooth, glabrous, opaque, pale-avellaneous, margin even, entire; context membranous; lamellae sinuate with decurrent tooth, broad, inserted, distant, pallid, toothed; spores ovoid, smooth, hyaline, 1–guttulate, about 5 × 3μ; cystidia none; stipe equal, smooth, glabrous, shining, white, 2.5 cm. long, scarcely 1 mm. thick. The entire hymenophore changes to pale-lilac on drying.

Type collected by W. A. Murrill on the ground in mixed woods just east of Gainesville, Fla., Oct. 29, 1938 (*F 18379*). A rare species, springing a surprise by its entire change of color.

Prunulus taxodii sp. nov.

Pileo conico-convexo, caespitoso, 1–1.5 cm. lato, nigro ad umbrino, sulcato; sporis 4–6 × 3–4μ, stipite subconcolori, 3 × 0.1 cm.

Pileus conic to broadly convex, often slightly umbilicate or truncate, cespitose or closely gregarious, 1–1.5 cm. broad; surface glabrous, black when young, umbrinous or fumosous in the older stages, distinctly sulcate-striate to the small central disk, which is very rugose; margin straight, entire, paler; context very thin, blackish, mild, odorless; lamellae adnate, broad, ventricose, inserted, distant, interveined, entire, cinereous, blackish near the context, blackening when bruised but not bleeding; spores irregular, subglobose to ellipsoid, smooth, hyaline, granular, 4–6 × 3–4μ; stipe equal, smooth, glabrous, whitish-shaggy at the base, blackish to avellaneous, not bleeding, about 3 × 0.1 cm.

Type collected by W. A. Murrill on the base of dead standing trunks of pond cypress in a cypress bog near Orange Heights, Alachua Co., Fla.,

Nov. 9, 1938 (*F 18376*). The trees were killed by a grass fire during a drought. So far as I now remember these are the first specimens of *Mycena* to be reported on *Taxodium* in America. Their color is quite peculiar; while the fresh spores suggest dried English peas.

Geopetalum viticola sp. nov.

Pileo semiresupinato, 3–7 mm. lato, striato, pallido; lamellis adnatis, praelatis, sporis ellipsoideis, 5–6 × 4μ.

Pileus broadly sessile, semiresupinate, closely gregarious, the reflexed portion thin, dimidiate, projecting 2–4 mm. and 3–7 mm. broad; surface glabrous, white-tomentose behind, distinctly striate over the gills, opaque-white, margin entire to rimose; context membranous, white, fleshy, fragile when dry; lamellae adnate, very broad, distant, inserted, pallid, edges uneven at times; spores broadly ellipsoid, apiculate, smooth, hyaline, 5–6 × 4μ; cystidia none.

Type collected by West and Murrill on a dead grape-vine near the ground at Arredonda, Fla., July 29, 1938 (*F 18317*). Dozens of hymenophores were examined, in all stages of development, but not one was found entirely resupinate nor was there a trace of a stipe in the entire lot.

NEW COMBINATIONS

For those using Saccardo's nomenclature the following new combinations are made:

Coltricia Mowryana = **Polystictus Mowryanus**
Galerula alachuana = **Galera alachuana**
Geopetalum viticola = **Pleurotus viticola**
Gymnopilus subdryophilus = **Flammula subdryophila**
Hydrocybe subminutula = **Hygrophorus subminutulus**
Prunulus subepipterygius = **Mycena subepipterygia**
Prunulus syringescens = **Mycena syringescens**
Prunulus taxodii = **Mycena taxodii**

Herbarium Florida Agricultural Experiment Station
Gainesville, Florida

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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